SEASONAL DYNAMICS OF SOCIAL SPACING AND MATE CHOICE IN ULVARIA SUBBIFURCATA

PATRICIA JILL HAMBROOK

SEASONAL DYNAMICS OF SOCIAL SPACING AND MATE CHOICE IN *Ulvaria subbifurcata*

BY

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ABSTRACT

The seasonal dynamics of aggression and social spacing; and mate choice of the radiated shanny, Ulvaria subbifurcata was examined using both laboratory and field observations. In addition, the role of aggression was examined in the context of territoriality and reproduction.

A 12 month study demonstrated adult U. subbifurcata hold and defend a crevice site year-round. Hence, adults can be considered territorial. The field study also demonstrated that adults hold and defend crevice sites from April to November. However, adult U. subbifurcata moved slightly offshore during winter months (December to March). Although not observed, it is suspected that while offshore adults also hold territories. It is thought that territoriality in U. subbifurcata is for shelter and reproduction.

The laboratory and field observations also demonstrated that aggression in both sexes increased during the pre-reproductive period (March to May) and peaked during the reproductive period (May to July). A proportion of the increase in aggression in the pre-reproductive period can be attributed to territory establishment in the field. However, the increase in aggression during the reproductive period can be attributed to increased GSI and hormonal

levels. Hence, aggression is important in the reproductive behaviour of the radiated shanny.

To examine the role of aggression in reproduction in U. subbifurcata additional laboratory and field observations were performed. Observations indicated that there was variance in male spawning success. It was discovered that a high level of male aggression and large body size were both important criteria for female mate choice and subsequent male spawning success. Laboratory observations also indicated that female choice of spawning partners was based on active examination of all experimental males and nest sites before spawning. In addition, field observations indicated positive assortative mating.

Aggression in U. subbifurcata changes temporally and appears to play an important role in territoriality and sexual selection, two important aspects of sociability.

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GENERAL INTRODUCTION

An area of evolutionary ecology that has been of considerable interest since Darwin (1871) is mating strategies in sexual selection. He proposed that individuals who do not differ in their ability to survive may differ greatly in their breeding success. Darwin (1871) proposed that breeding success depends on intrasexual selection, competition within one sex for members of the opposite sex, and intersexual selection, choice by individuals of one sex for particular members of the opposite sex. Bateman (1948) and later Trivers (1972) stated that sexual selection is governed by the relative parental investment of the two sexes. Trivers (1972) defines parental investment as any investment by a parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring. Parental investment by either sex will tend to result in the sex investing the least in offspring competing to mate with the sex investing the most. The sex who invests more is predicted to be choosy of its mating partners since it has more to loose from a inappropriate mating.

Trivers (1982, 1985) points out that females are generally the sex which invests the most in offspring.

Females are thought to invest considerable amounts of metabolic energy in the production of a given sex cell, the egg, whereas males invest considerably less in sperm production (Bateman 1948, Trivers 1972). Because of the initial high cost of eggs, females tend to increase their parental investment beyond gamete production by gestation and suckling to enhance survival of the offspring; thus, maximizing past reproductive investment in the egg (Orians 1969). Alternatively, males are generally believed to be reproductively limited only by the number of females they can fertilize (Bateman 1948; Trivers 1972). Hence, classic research on sexual selection has concentrated on organisms in which females are the choosier sex and males compete among themselves for females (Bateman 1948; Trivers 1972; Cox and LeBoeuf 1977; Partridge et al. 1987).

In organisms in which male parental investment increases beyond gamete production to mate-, nest-guarding, and paternal care of the offspring, males are expected to exhibit some degree of mate choice (Trivers 1972). In organisms in which male parental investment per offspring is higher than female investment, males are expected to be choosier in mate selection than females (Gwynne 1981; Petrie 1983; Trivers 1985). Among organisms in which parental care by the two sexes is comparable, both males and females are expected to exhibit choice, hence, the reproductive success of the two sexes is expected to vary in similar ways (Petrie

1983).

The benefits that animals may derive by choosing a particular mate range from the long-term advantage of mating with an individual of high genetic quality to immediate gains such as courtship feeding (Partridge and Halliday 1984). From an evolutionary perspective, the ultimate benefit of choice is the increase in an individual's fitness (Partridge and Halliday 1984). Despite theoretical advances in understanding sexual selection derived from population models (e.g. O'Donald 1980; Kirkpatrick 1982; Seger 1985), field experiments (e.g. Andersson 1982), and breeding studies (e.g. Majerus et al. 1986; Simmons 1987), fundamental questions in sexual selection are still unanswered (Partridge 1986). For example, the rules females use to choose mates and the mechanisms of choice are still unknown (Partridge 1986). In addition, traits important in sexual selection are essentially unstudied outside of the reproductive context.

Sexual selection studies have concentrated on mammals, birds, insects, and reptiles (e.g. Trivers 1976; Cox and LeBoeuf 1977; Smith 1980; Partridge et al. 1987). There is an increasing awareness that the behaviour of teleost fishes is not a simplified version of that seen in birds and mammals (e.g. Pitcher 1986). There are well over 22,000 living species of teleosts, including nearly all those of importance in commercial fisheries and aquaculture (Bond

1979). Teleosts are represented in almost every aquatic environment from temporary desert pools to deep oceans (Bond 1979). For teleosts, 'behavioural plasticity is one of the keys to their success' (Pitcher 1986). Moreover, fishes exhibit enormous diversity in both their reproductive modes and the types of parental care they provide (Gross and Sargent 1985). In those fishes with parental care, paternal care dominates (Breder and Rosen 1966). Male parental ability has been shown to be important in female mate choice in some fish species (Brown 1981; Grant and Colgan 1983; Keenleyside et al. 1985).

The present study examines seasonal dynamics of aggression and social spacing, and mate choice in the radiated shanny, Ulvaria subbifurcata, a nocturnal Northwest Atlantic stichaeid. Female radiated shannies deposit eggs in the males' nest sites where they are left to be guarded and aerated by the male until they hatch as planktonic larvae (LeDrew and Green 1975). Female choice of spawning partners may occur since LeDrew and Green (1975) found some males guarding more than one egg mass, while other males had no eggs. Homing studies have indicated adults occupy defended sites during the reproductive season (May - June; Fisher 1972); however, the dynamics and function of this space usage is unclear. Consequently, Ulvaria subbifurcata offers an opportunity to examine aggression and social spacing and its association with reproduction. This study

is divided into 2 chapters: 1) Seasonal dynamics of aggression and social spacing; and 2) Mate choice. The first chapter will discuss a year-long study examining aggression. The role of aggression is examined with respect to territoriality and reproduction. The second chapter examines, more specifically, the role of aggression in reproduction, particularly in female mate choice.

CHAPTER 1 SEASONAL DYNAMICS OF AGGRESSION AND SOCIAL SPACING

1.1. Introduction

Agonistic behaviour plays an important role in social behaviour (Ovaska 1987) as it can influence social spacing (territoriality), dominant/subordinate hierarchies, sexual selection, and predatory behaviour (Wilson 1975). According to Reese (1978) space related or territorial behaviour is one of the most important determinants of social behaviour in animals. It is through social spacing that many other aspects of social behaviour, such as reproduction, can be affected and governed (e.g. Hixon 1987).

Territoriality occurs when an individual defends an area against others, thereby gaining increased access to included resources (Kaufman 1983). There has been considerable dispute on the precise definition of territoriality; specifically on the subject of exclusiveness of the space, and the overtness of the aggression to maintain the space (i.e. Brown and Orians 1970; Morse 1980; Kaufman 1983). Regardless of the disputable definitions of territoriality, the nature and the function of territoriality are better reconciled. Space acquisition cannot be achieved or maintained without dominance/subordinance. Dominance/subordinance is a relationship between two individuals in which one (the subordinate)

defers to the other (the dominant) in contest situations (Kaufman 1983). Territoriality is composed of two continuous components, space and time (Kaufman 1983). Much research has examined only the physical components of the territory and its owner (e.g. Hurly and Robertson 1984). However, territories vary in the length of time during which they exist. For example many animals only defend territories during the breeding season for acquisition of mates (e.g. Salamanders- Ovaska 1987). In addition, territory size and dominance/subordinance relationships have been noted to change temporally (Kaufman 1983).

Aggression is necessary for the establishment and may be used, but not necessary, for the maintenance of territories. Since territories determine the usage of space by a group of animals, aggression can play a very important role in the spacing and ultimate social interactions of animals. Despite the enormous literature on the function of aggression in territoriality little work on aggression has gone beyond spacing to the overall social behaviour of the animal; few studies have examined the changes in seasonal aggression and how it is related to changes in territorial and reproductive behaviour, two very important aspects of sociability (cf. Hixon 1987). Furthermore, traditional work on aggression and social spacing has been on birds or mammals. Not until recently have patterns of aggression and spatial use been widely noted in solitary and

territorial fish (Cole 1984). This study examines the seasonal dynamics of aggression and social spacing and its association with the reproductive behaviour of Ulvaria subbifurcata.

Besides work done by Fisher (1972), and Goff and Green (1978) little is known about the aggressiveness, site tenacity, and territoriality of Ulvaria subbifurcata. The existence and function of territoriality in Ulvaria subbifurcata is unclear. No quantitative evidence exists for territoriality in U. subbifurcata. Fisher (1972) found no evidence to support the possibility of territoriality in Ulvaria subbifurcata except during the spawning season when agonistic behaviour was noted, but not quantified for males. Fisher (1972) found that both males and females have a restricted home range (an area that an animal habitually patrols), on the order of 2-3 m^3. It may be identical to a territory or it can be larger (Burt 1943). Fisher (1972) suggests the function of the home range to be a means of "adequate spacing" as well as guaranteed shelter from predators. In addition, small offshore migrations have been observed in Ulvaria subbifurcata (Green, pers. comm.), but migration has not been recorded with changes in aggressiveness or reproduction.

Over a 12 month period I used both laboratory and field observations to examine the seasonal dynamics of aggression and social spacing. More specifically this project

addressed the following questions: 1) Is Ulvaria subbifurcata a territorial fish and does territoriality occur year-round?; 2) Does aggression in U. subbifurcata vary temporally and is this variation associated with changes in space usage or territoriality? 3) Is the variation in aggression and space usage associated with reproduction in U. subbifurcata?

1.2. Methods

1.2.1. Laboratory Observations

Adult Ulvaria subbifurcata were collected by SCUBA from Portugal Cove (47 37'N, 52 56'W), Newfoundland in May 1986. Fish were maintained in a holding aquarium (90 X 70 X 40 cm; 252 l) at ambient water temperature and photoperiod until October 1986 (yearly means: water $\bar{x}$= 3.8° C; photoperiod $\bar{x}$=10.5 hours of light). Males and females were separated in the holding aquarium by a mesh partition and were fed every two to three days with brine shrimp, capelin, and amphipods (when available).

Two aquaria (120 X 40 X 35 cm; 168 l) were placed in a blackened room with reversed ambient photoperiod to enable observations during the day. Dusk and dawn, and day and night were completely reversed in the experimental room. Dusk and dawn (1 hr each) were simulated by a 25W frosted bulb located centrally above each aquarium, and day was simulated by two 60W bulbs located centrally above each aquarium. Two 25W red bulbs evenly placed above each aquarium enabled observations to be made during the simulated dark hours. Green et al. (1988) found no effect of reversed photoperiod or red light on the agonistic and reproductive behaviour of the radiated shanny. Furthermore, studies have indicated animals do not use absolute levels of light and dark to cue daily rhythms, but rather use relative amounts of light and dark (Williams 1976). Twice a month

for 12 months the photoperiod was adjusted to replicate ambient photoperiod. Each aquarium had 1 cm of gravel covering the bottom mimicking substrate where the shanny naturally occurs (pers. obs.), and each aquarium contained four crevices made from two equal-sized overlapping rocks. All four crevices were similar in size of rocks and in volume.

Observations were made on eight, sexually mature individuals once every two weeks for a year (October 1986-September 1987). Four individuals were used per aquarium (similar sized ±0.2 cm in total length). Mean distances between crevices in aquaria were similar to those observed in field studies ($\bar{X}$ = .5m; range 1.5 - .2m). Initially, each aquarium contained two males and two females of similar size. However, due to deaths of six individuals (because of supersaturation) during January 1987, individuals were replaced with fish of similar size, but of unknown sex from the holding aquarium. The effects of these additions were minimal as discussed in results. Sex could only be determined visually in April and May when spawning colourations of each sex develops (Mathisen 1979; Green et al. 1988). After the death of an individual and at the end of the observational period, individuals were measured (total length), sexed by gonadal examination, and aged by otoliths.

Observations on each aquarium were made for 30 min at:

1) dusk, 2) midnight, 3) dawn, and 4) midday. All observations were recorded with a NEC event recorder. At the onset of each recording session water temperature and initial position of all individuals were noted using the all occurrence technique (Lehner 1979). This technique was used since the agonistic behaviour of the fish did not occur more often than the observer could record them. The total time an individual spent out of its home site was also recorded. A crevice was considered a home site when an individual was repeatedly observed in it (over 75% of the time). During each session all aggressive encounters were recorded. An aggressive encounter was defined as a behavioural interaction between two fish which ended in one displaying an aggressive posture and the other displaying a submissive posture (see Appendix I for description of postures). An aggressive encounter may have begun with both fish displaying aggressive postures, but the final outcome resulted in one fish 'backing down' and displaying a submissive posture. Aggressive encounters were described by: 1) identity and status of the fish involved; 2) duration and; 3) intensity of the aggressive encounter; and 4) time spent out of the crevice site. Intensity of aggression was scored as 1, if one individual (aggressor) had an erect dorsal fin, head elevated, operculum flared; 2, if a fish lunged at the opponent with mouth open; or 3, if one fish individual made contact with the other individual.

To examine the seasonality of aggression the year was divided into pre-reproductive, reproductive, and non-reproductive periods. The pre-reproductive period begins in late March/early April when shanny gonadal somatic index (GSI) begins to increase (LeDrew and Green 1975). The reproductive period begins in May and ends in July. At this stage GSI is at its peak in all individuals, males are spawning and egg guarding, and females are in a gravid condition or spawning. Post-reproductive state begins in July and ends in February. At this point both sexes are reproductively spent and are in gonad recovery (LeDrew and Green 1975).

Habituation may occur between individuals in the same aquarium. However, in the field, neighbours remain permanent throughout April to October (see Results); thus, permanent neighbours appear to mimic natural conditions. Experimental fish were fed every two to three days with brine shrimp, capelin, and amphipods (when available).

Before data of the fish from both aquaria were pooled for analyses differences in daily and annual means of all measures of aggression were examine using student's t-test after square root transformation. Also, trends in aggression levels throughout a daily cycle was examine by an ANOVA. Finally, the effects of sex and temperature, and sex and date were examined using a two-way ANOVA of the daily means. The level of significance was 0.05 for all

statistical tests.

All aggressive encounters were categorized into four pairings; female displaying aggression to a female, female displaying aggression to a male, male displaying to a female, and male displaying to a male. Comparisons were made between the four categories using a student's t-test. Comparisons were also made between reproductive and non-reproductive periods (summation of pre- and post-reproductive periods) within each group using a chi-square test.

1.2.2. Field Observations

Field observations were carried out at Bellevue (43 38'N, 53 43'N), Trinity Bay, Newfoundland, in a shallow cove (maximum depth 2 m at low tide) at the mouth of the estuary known as Broad Lake (Figure 1). In April 1986, a study site was established in the mouth of Broad Lake, running NE to SE. The site was in a natural depression (approximately 1.5m x 9m), containing high densities (1.05/m^2) of shannies. The site was surveyed once per month except during April to July, when the site was surveyed each week. Number, size (total length), sex and crevice sites of the shannies in the site, and substrate of each crevice site were noted. Substrates were define as 1) 100% rubble (rock

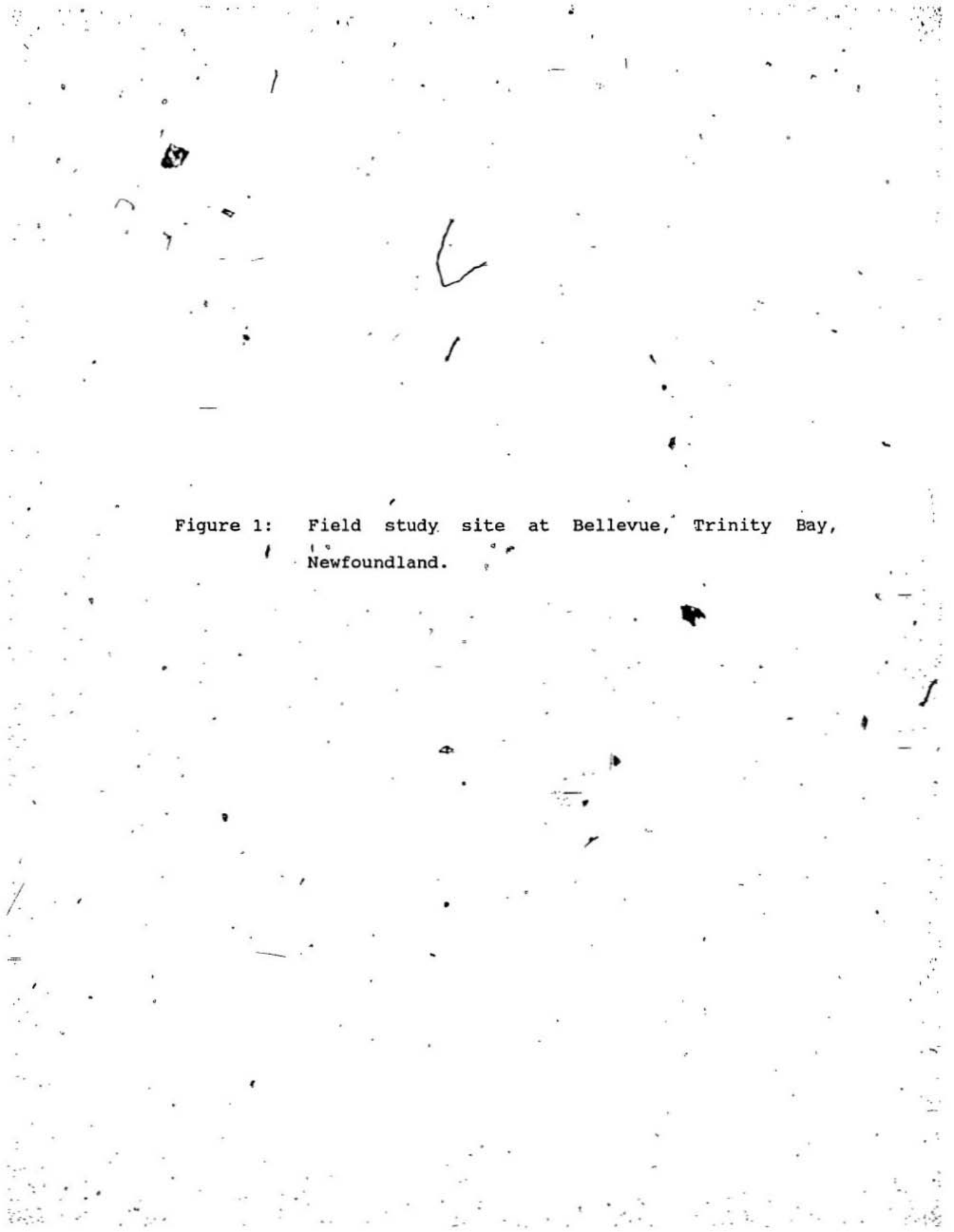
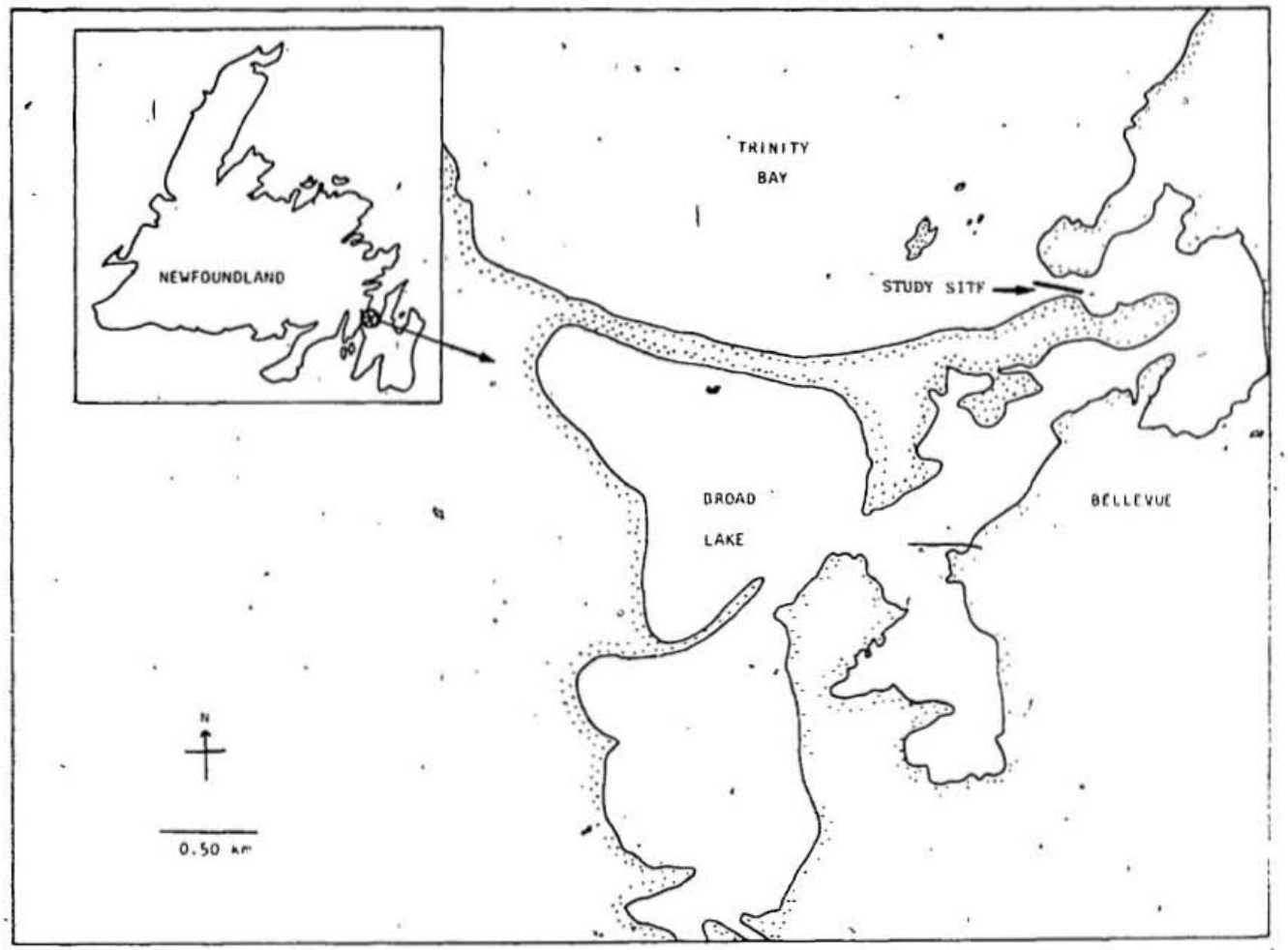


Figure 1: Field study site at Bellevue, Trinity Bay, Newfoundland.


NEWFOUNDLAND
TRINITY
BAY
STUDY SITE
BROAD
LAKE
BELLEVUE
N
0.50 km

15(b)

less than 1 cm in diameter), 2) a mixture of rubble and boulder, or 3) 100% boulders. Fish total lengths were estimated by placing a ruler on the substrate next to each fish. Mature individuals were sexed when spawning colours and gravidness became apparent in May. Individual body-markings were noted for later identification. During each dive the crevice in which each shanny was positioned was recorded on maps of the transect.

Five adult males and five adult females were tagged in August 1986. Coloured beads were attached below the dorsal fin, through the epaxial musculature midway between the head and caudal fin by monofilament thread. Over one year the site was surveyed for tagged fish. An estimate of activity levels was determined by swimming on the surface over the site for 10 min and recording the number of individuals outside their home sites. The site was surveyed during late afternoon or dusk to control for behavioural differences due to photoperiod. Ideally, the site should have been surveyed during the same four periods when the laboratory observations were performed; however, strong currents with back eddies during tidal flux made field observations impossible except during ebb tide.

In order to determine temporal or sexual variation in aggression levels, a model presentation experiment was performed during each dive, commencing June 1986. A model male intruder was constructed by freeze-drying a large male

(larger than the mean total length of the adult population $\bar{x}$ 7.23cm) in an aggressive posture (i.e. fins erect, head elevated). The model was gutted, shellacked, and mounted on a stick. Methodology of presentation followed that of Colgan et al. (1981). During each test the model was presented to a male six times. Each presentation involved moving the dummy horizontally and broadside at a constant speed (15sec/m) towards the crevice, pausing for three sec at the mouth of the crevice, then withdrawing the model at the same speed. The model was removed from the view of the test fish for 2-3 sec between each presentation. The occurrence and distance of each response to the intruder by the male was recorded. Response distance was estimated by placing a weighted metre stick in front of the nest prior to testing. The model was presented to five males and to five females during the monthly survey for a 12 month period. The five males and females were the same from June to November 1986; however, when individuals returned to study site in April 1987 (see section 1.3.2) identity of individuals could not be guaranteed. Hence, an additional group of five males and five females were used from April to July 1987.

Both the number and the distance of response were compared between sexes using a student's t-test. Comparisons among the three reproductive periods were made using an F-test after testing for normality. Also, habituation of residents to the model intruder during the 6

presentations was examined by a comparison of the first two introductions and the last 2 introductions using a student's t-test. The level of significance was 0.05 for all statistics

1.3. Results

1.3.1. Laboratory Observations

Fourteen fish were observed during the study. From October 1986 to January 1987 each aquarium contained two males and two females of similar size and age (See Appendix 2). However, from January 1987 to September 1987 one aquarium contained three males and one female while the second aquarium contained two males and two females (Appendix 2). During May 1987, a spawning occurred in the tank containing two individuals of each sex.

The fish in each aquarium were not significantly different from each other in daily or annual means of number of aggressive encounters per observation period (MTOT), duration of encounters (MDUR), intensity of encounters (MINT), and time spent out of the crevice per observation period (MTSN) (students t-tests; Table 1). Consequently, for further analyses the data of the fish from both aquaria were pooled.

Aggression as measured by the number of aggressive encounters, differed significantly among mid-day, dawn, dusk, and mid-night respectively (ANOVA; $F=6.11$, $df=1,3$, $p=0.05$). The trend was an increase from mid-day to mid-night. During mid-night there were significantly more aggressive encounters than during all other times (Chi-square: midnight vs: 1) mid-day, $X^2 = 14.67$, $N=24$; 2) dawn,

Table 1: Comparisons of the monthly and annual means of the total number of aggressive encounters (MTOT), intensity (MINT), duration of encounters (MDUR), and time spent out of crevice (MTSN) among laboratory-held fish. Standard errors in parentheses. Note comparisons were made on square root values.

DATE	TANK 1				TANK 2			
	MTOT	MINT	MDUR	MTSN	MTOT	MINT	MDUR	MTSN
OCT 1986	.21 (.17)	1.25 (.25)	20.59 (6.32)	12.63 (1.46)	.58 (.44)	1.28 (.15)	27.01 (6.41)	19.39 (3.59)
NOV 1986	.39 (.10)	1.33 (.33)	3.77 (.46)	4.50 (2.33)	.50 (.22)	1.10 (.10)	4.35 (.52)	9.69 (3.19)
DEC 1986	.12 (.09)	2.50 (.57)	14.65 (2.25)	6.16 (2.21)	.12 (.09)	2.60 (.50)	22.00 (7.40)	9.04 (2.85)
JAN 1987	.96 (.06)	2.00 (.00)	21.40 (6.00)	5.19 (1.69)	.93 (.09)	2.50 (.50)	21.90 (4.50)	5.89 (2.15)
FEB 1987	.15 (.11)	1.00 (.00)	18.63 (2.23)	6.82 (1.87)	.10 (.43)	1.00 (.00)	20.50 (10.96)	5.59 (1.16)
MARCH 1987	.20 (.19)	1.67 (.17)	19.22 (9.92)	5.04 (1.74)	.19 (.10)	1.33 (.33)	23.97 (6.56)	7.83 (1.96)
APRIL 1987	.38 (.16)	1.20 (.20)	22.32 (2.73)	7.56 (2.07)	.50 (.13)	1.88 (.29)	19.73 (2.98)	9.31 (2.75)
MAY 1987	.44 (.22)	1.83 (.29)	38.28 (2.79)	15.83 (2.96)	.63 (.26)	1.67 (.31)	38.86 (7.27)	14.37 (3.02)
JUNE 1987	.50 (.18)	1.58 (.27)	25.80 (2.95)	10.78 (3.05)	.80 (.34)	1.54 (.34)	28.48 (5.82)	12.58 (3.02)
JULY 1987	.13 (.12)	1.50 (1.00)	22.90 (12.01)	8.18 (2.67)	.38 (.10)	1.67 (1.41)	24.48 (11.14)	9.88 (2.83)
AUG 1987	.06 (.06)	1.00 (.00)	10.50 (9.00)	7.21 (2.67)	.07 (.10)	1.00 (.00)	13.70 (9.46)	8.34 (2.50)
SEPT 1987	.06 (.04)	1.00 (.00)	12.10 (6.58)	6.74 (2.27)	.13 (.09)	1.50 (.50)	11.85 (4.95)	8.89 (2.73)
YEAR	.22 (.31)	1.49 (.08)	20.29 (1.37)	6.75 (.49)	.31 (.04)	1.63 (.08)	24.17 (1.60)	7.41 (.56)
N	380	55	55	380	356	79	79	356

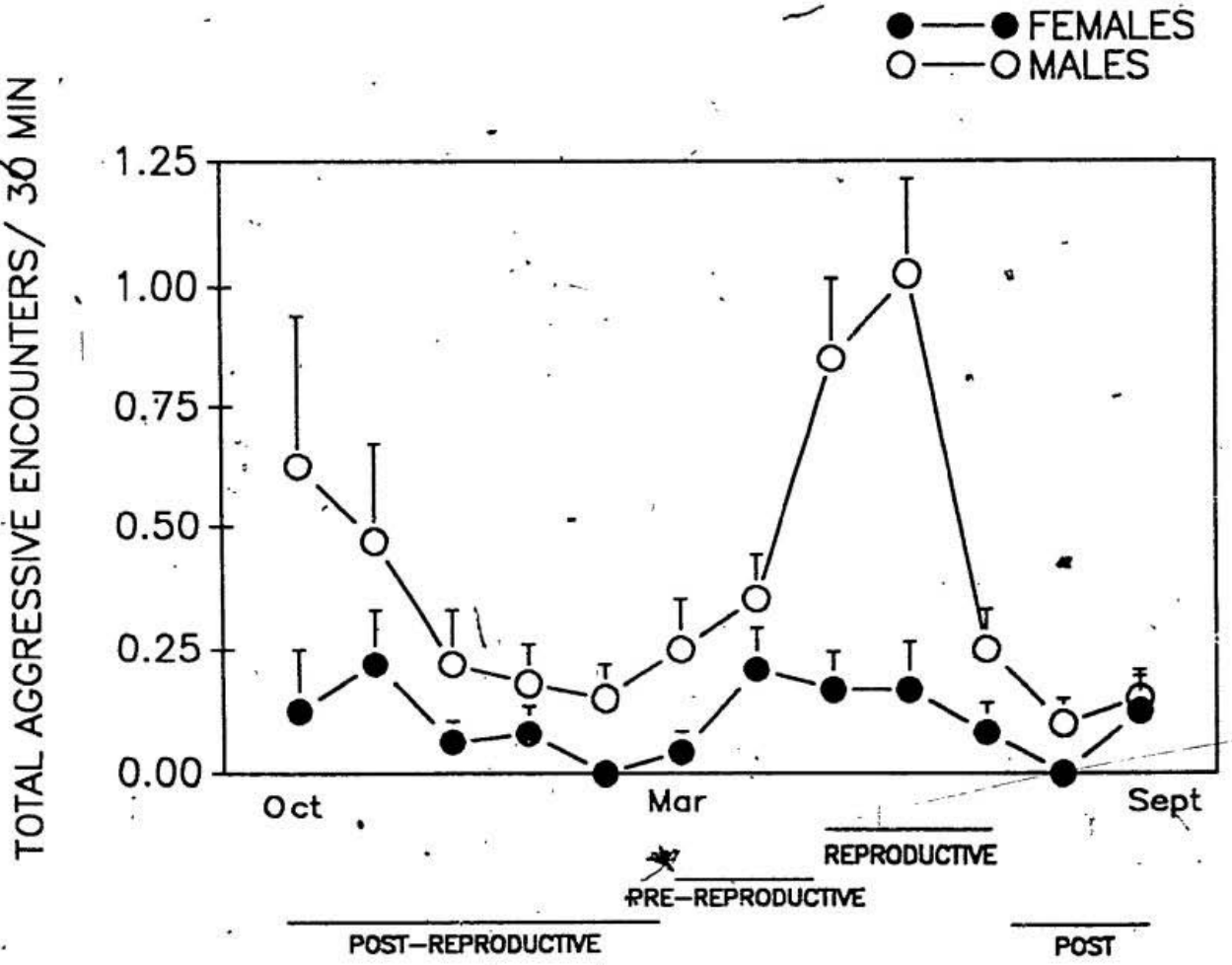
*****T-tests indicated no significant differences at the p=0.05 level in all variables between fish in each tank for each month. T-tests also indicated no significant differences at the p=0.05 level in all variables between fish in each tank over the entire year.

X^2 = 6.49, N=24; 3) dusk, X^2 = 7.43, N=24).

Seasonally, all four measures of aggression increased during the pre-reproductive state, with a peak of aggression occurring during the reproductive state (Figures 2-5; Table 2). There were also observed increases in all four measures of aggression at the onset of the observations in October 1986, and in January 1987 when dead fish were replaced with new fish. Overall, females were less aggressive than males in all four variables (Table 3). Both sex and temperature and sex and date had significant effects on all four aggression measures (Table 4). However, temperature alone had no effect on the mean total number of aggressive encounters nor the mean duration of aggressive encounters (Table 4). This is not surprising since similar sea temperatures exist during spring and fall; although very different patterns of aggression exists between the two periods, Date alone had significant effects on all four variables (Table 4).

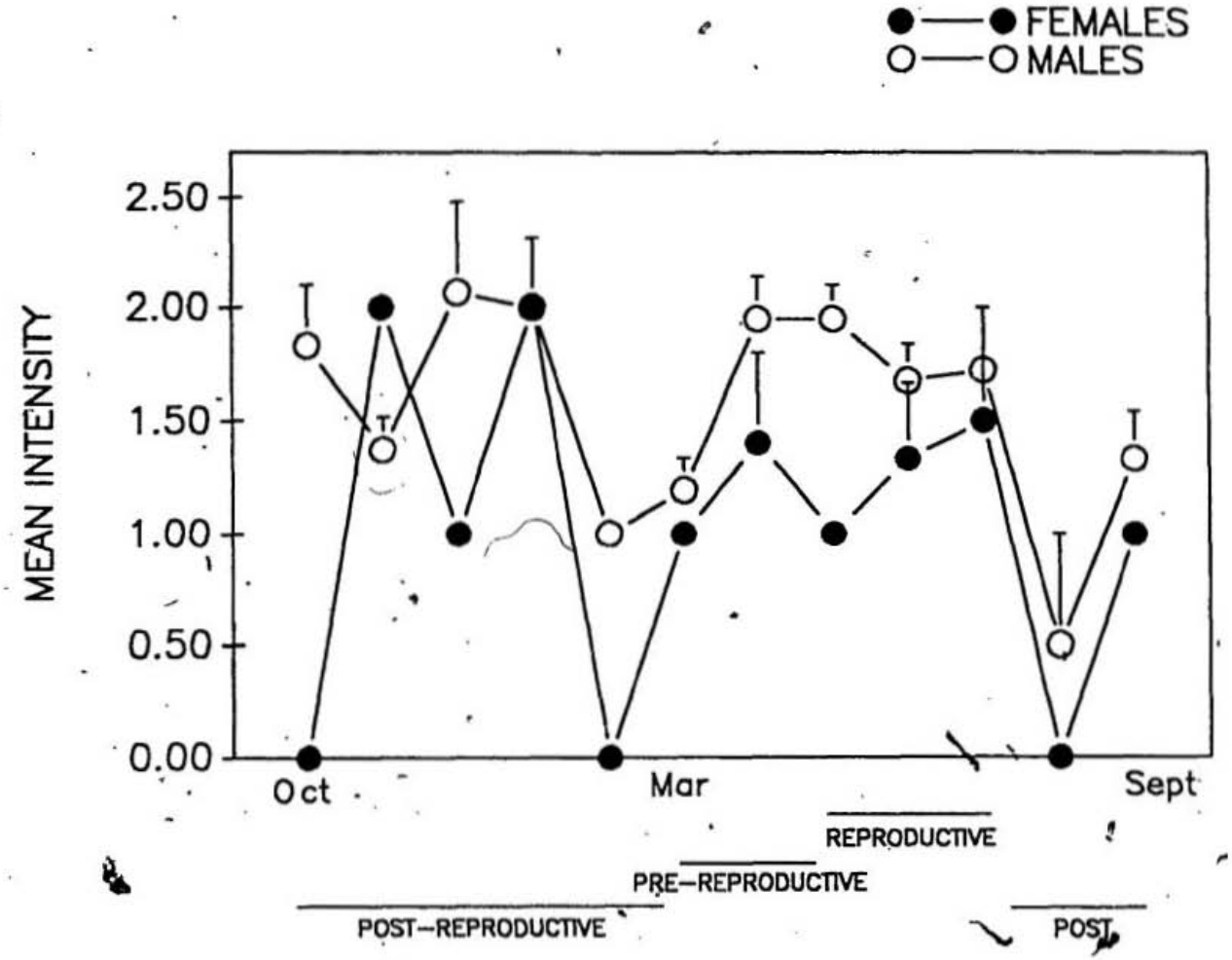
Comparison among the four categories of aggressive encounters indicated male to male interactions occurred significantly more often than all others (t= 14.61, df=1,3, p< 0.05). Male to female interactions decreased significantly during the reproductive state compared to the non-reproductive state (X^2 = 19.534, df=1, p< 0.001), and female to male interactions increased significantly during the reproductive period as compared to the non-reproductive

Figure 2: Mean total number of aggressive encounters per 30 min observation period for 12 month laboratory study. The 12 month period is divided into pre-, post-, and reproductive periods (See text for explanations of divisions). Standard errors denoted by vertical bars.


FEMALES
MALES
TOTAL AGGRESSIVE ENCOUNTERS/ 30 MIN
1.25
1.00
0.75
0.50
0.25
0.00
Oct
Mar
Sept
REPRODUCTIVE
PRE-REPRODUCTIVE
POST-REPRODUCTIVE
POST

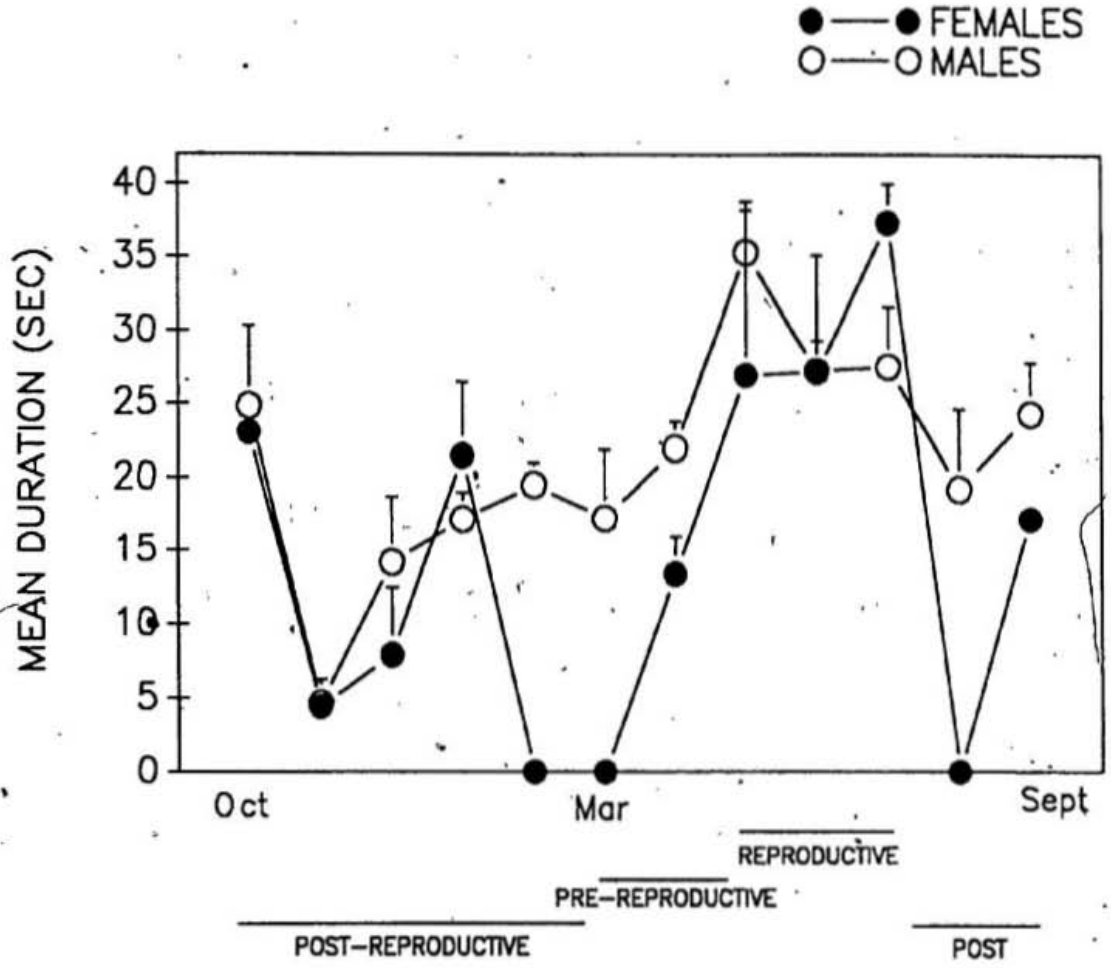
22 (b)

Figure 3: Mean intensity of aggressive encounters over 12 month laboratory study. Year represented as in Figure 2. Standard errors denoted by vertical bars.


FEMALES
MALES
MEAN INTENSITY
2.50
2.00
1.50
1.00
0.50
0.00
Oct
Mar
Sept
REPRODUCTIVE
PRE–REPRODUCTIVE
POST–REPRODUCTIVE
POST

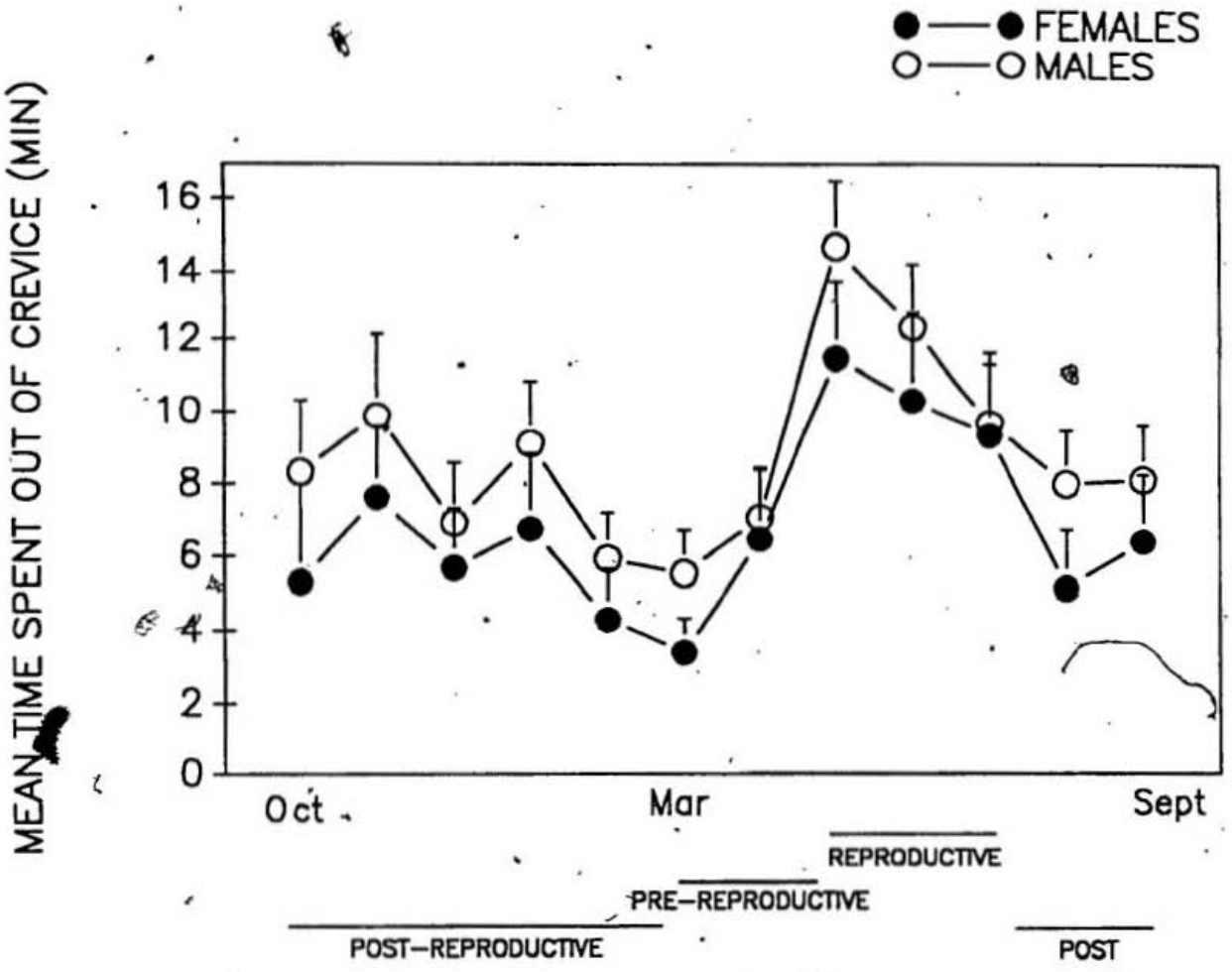
23(b)

Figure 4: Mean duration (sec) of aggressive encounters per observation period over 12 month laboratory study. Year represented as in Figure 2. Standard errors denoted by vertical bars.


FEMALES
MALES
MEAN DURATION (SEC)
40
35
30
25
20
15
10
5
0
Oct
Mar
Sept
REPRODUCTIVE
PRE–REPRODUCTIVE
POST–REPRODUCTIVE
POST

24 (b)

Figure 5: Mean time spent out of crevice site per 30 min observation period over 12 month laboratory study. Year represented as in Figure 2. Standard errors denoted by vertical bars.


FEMALES
MALES
MEAN TIME SPENT OUT OF CREVICE (MIN)
16
14
12
10
8
6
4
2
0
Oct
Mar
Sept
REPRODUCTIVE
PRE–REPRODUCTIVE
POST–REPRODUCTIVE
POST

25 (b)

Table 2: Comparisons among the pre-, post-, and reproductive periods in the mean total number of aggressive encounters (MTOT), mean intensity of encounters (MINT), mean duration of encounters (MDUR), and mean time spent out of crevice (MTSN) among laboratory-held fish.

PERIODS	AGGRESSIVE MEASURES			
	MTOT	MINT	MDUR	MTSN
REPRODUCTIVE VS PRE-REPRODUCTIVE	24.0*	26.0*	23.0*	25.0*
REPRODUCTIVE VS POST-REPRODUCTIVE	69.0*	67.0*	72.0*	68.0*
PRE-REPRODUCTIVE VS POST-REPRODUCTIVE	55.0*	49.0*	51.0*	47.0*

* indicates $p < 0.05$ (Mann Whitney test).

Table 3: Comparison of mean values of four aggressive measures between male and female laboratory-held fish.

AGGRESSION VARIABLE		MEAN	N	S.E.	F	p
MTOT	♀	0.11	96	0.02	4.89	<.001
	♂	0.37	96	0.04		
MINT	♀	1.29	28	0.10	3.67	.027
	♂	2.65	106	0.07		
MDUR	♀	17.65	28	2.58	4.21	.048
	♂	26.88	106	1.20		
TSN	♀	6.87	96	0.57	5.13	.025
	♂	10.82	96	0.49		

MTOT= mean number of aggressive encounters per 30 min observation period.
MINT= mean intensity of aggressive encounters.
MDUR= mean duration (sec) of aggressive encounters.
MTSN= mean time (min) spent out of crevice per 30 min observation period.
N= number of 30 min observation periods,
S.E.= standard error of the mean.

Table 4: Effects of sex and temperature, and sex and date, on mean total number of aggressive encounters (MTOT), mean intensity of encounters (MINT), mean duration of encounters (MDUR), and mean time spent out of crevice (MTSN) among laboratory-held fish.

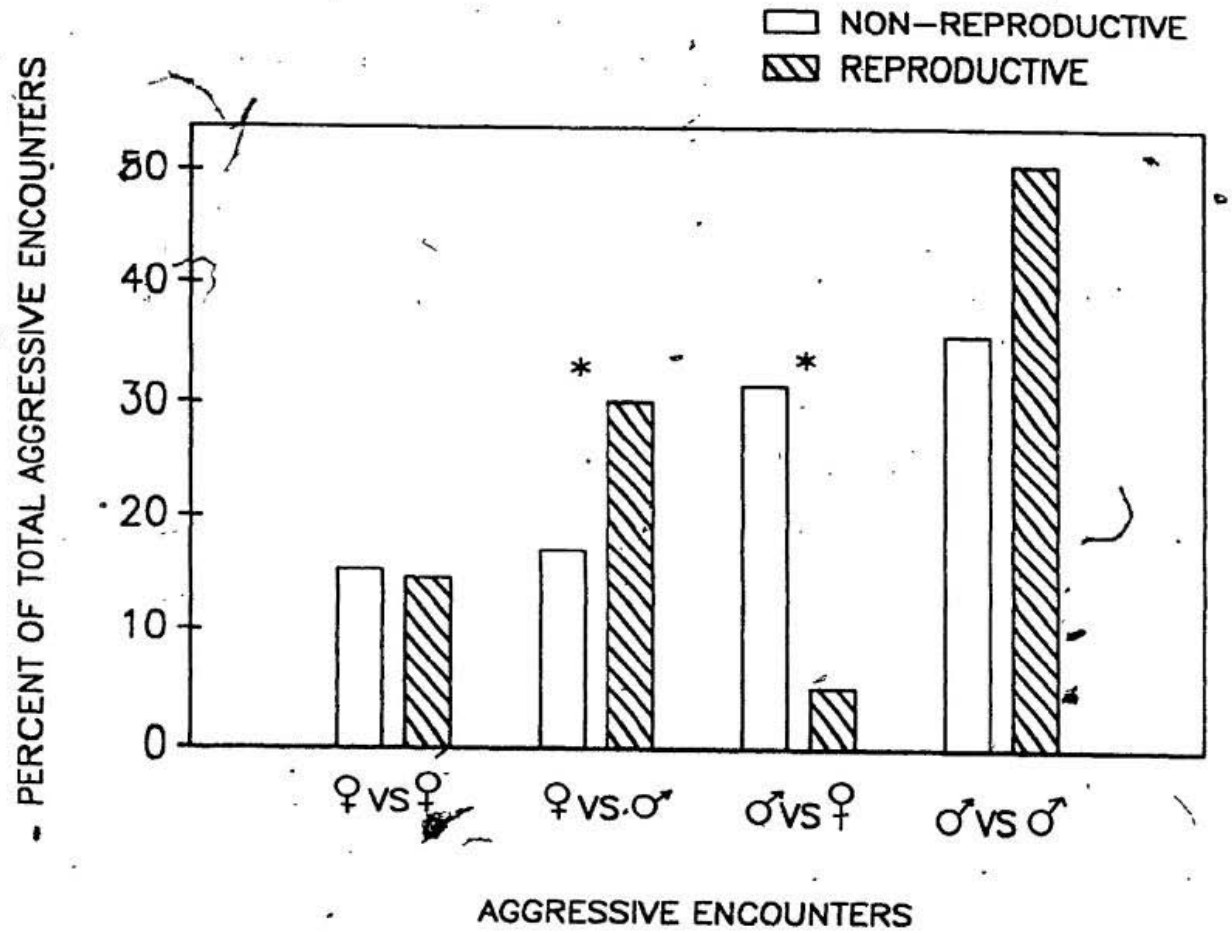
TWO- WAY ANOVA

SOURCE OF VARIATION	F MTOT	MINT	MDUR	MTSN	d.f.
SEX AND TEMP	7.79**	8.51**	12.25**	4.84**	1,9
SEX	31.03**	30.69**	31.98**	8.14**	1
TEMP	5.18**	0.01	1.99	4.29*	9
INTERACTION	2.17*	3.09*	3.70*	0.23 *	9
SEX AND DATE	4.60**	5.04**	7.66**	3.21**	1,23
SEX	22.80**	24.57**	24.08**	6.53*	1
DATE	3.59**	3.94**	6.66**	3.02*	23
INTERACTION	1.24*	1.73*	2.08*	1.72*	23

* indicates p<0.05.
** indicates p<0.01.

Figure 6: Comparisons between the reproductive and non-reproductive periods of the number of aggressive encounters among ♀ vs ♀, ♀ vs ♂, ♂ vs ♀, and ♂ vs ♂ during a 12 month laboratory study. * t-test; $p<0.05$; ** X^2; $p<0.05$.

29(b)


NON–REPRODUCTIVE
REPRODUCTIVE
PERCENT OF TOTAL AGGRESSIVE ENCOUNTERS
50
40
30
20
10
0
*
*
♀VS♀
♀VS♂
♂VS♀
♂VS♂
AGGRESSIVE ENCOUNTERS

period (X^2= 3.87, df=1, $p<0.05$). Thus, males reduced the number of aggressive encounter with females, while females increased the number of aggressive encounters towards males during the reproductive period.

Finally, aggressive fish grew more in total length over the study period than less aggressive fish, regardless of sex (multiple regression; r=0.82, N=14, p= 0.016; Appendix 2).

1.3.2 Field Observations

In 1986, the Bellevue site contained 23 adult shannies; 11 males which spawned and guarded nests, two males which did not spawn, and 11 females which at one time showed gravidness (Figure 7; Appendix 3). In 1987, the Bellevue site contained 19 adult shannies, eight males which spawned and guarded nests, two males which did not spawn, and nine females which at one time showed gravidness (Figure 8; Appendix 3). In both years the sex ratios did not deviate from a 1:1 ratio (1986: X^2 = 0.04, df=1, $p>0.05$; 1987: X^2 = 0.05, df=1, $p>0.05$).

Adult shannies left inshore areas in late October/ early November 1986 ($\bar{x}$ water temperature = 1.0 ± 1.2°C) and returned inshore in late April 1987. During the onshore period in 1986 and 1987 adult shannies did not change

Figure 7: Bellevue, Trinity Bay, study site 1986. ● indicates one egg mass. Drawn figures denote boulders.

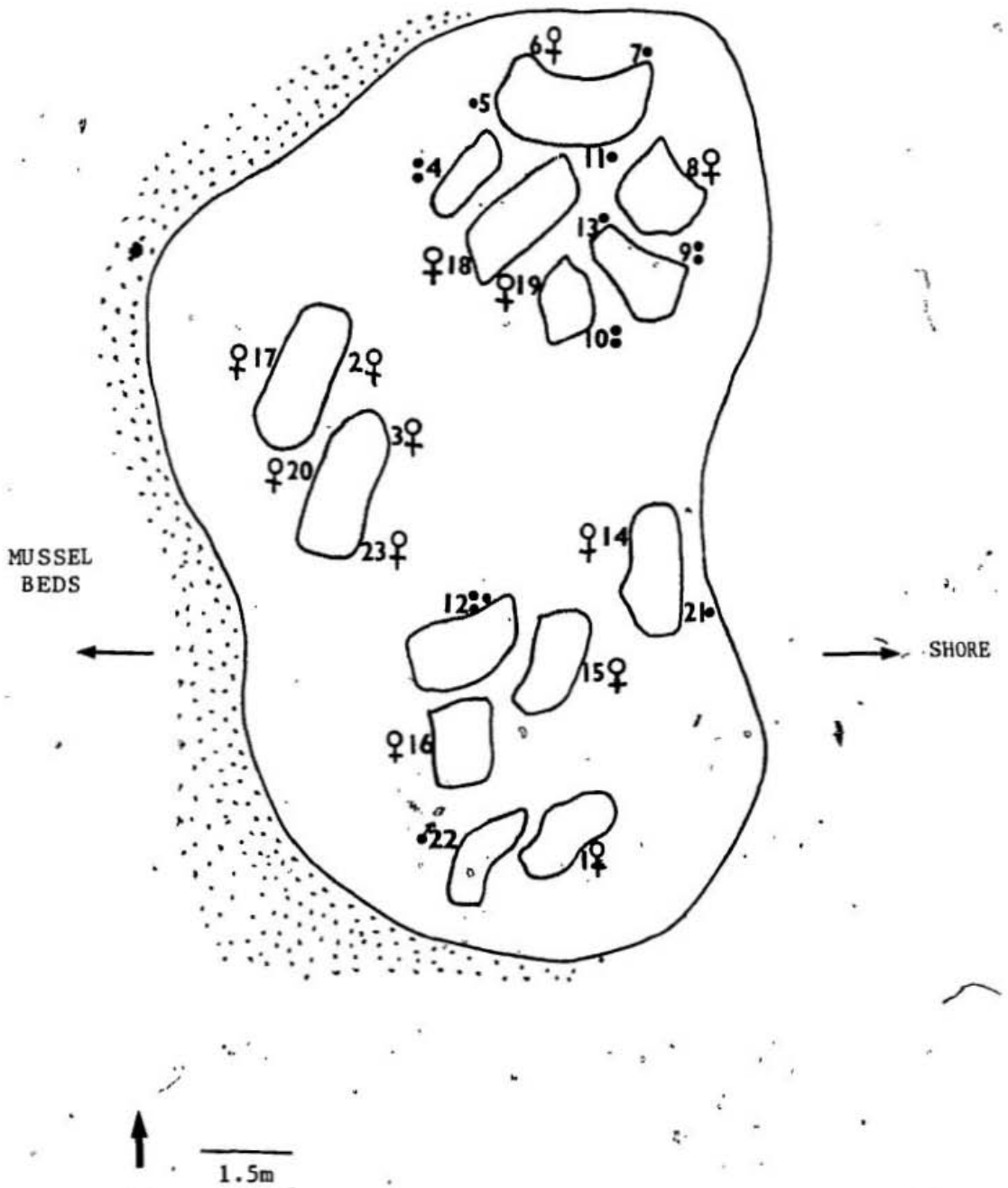
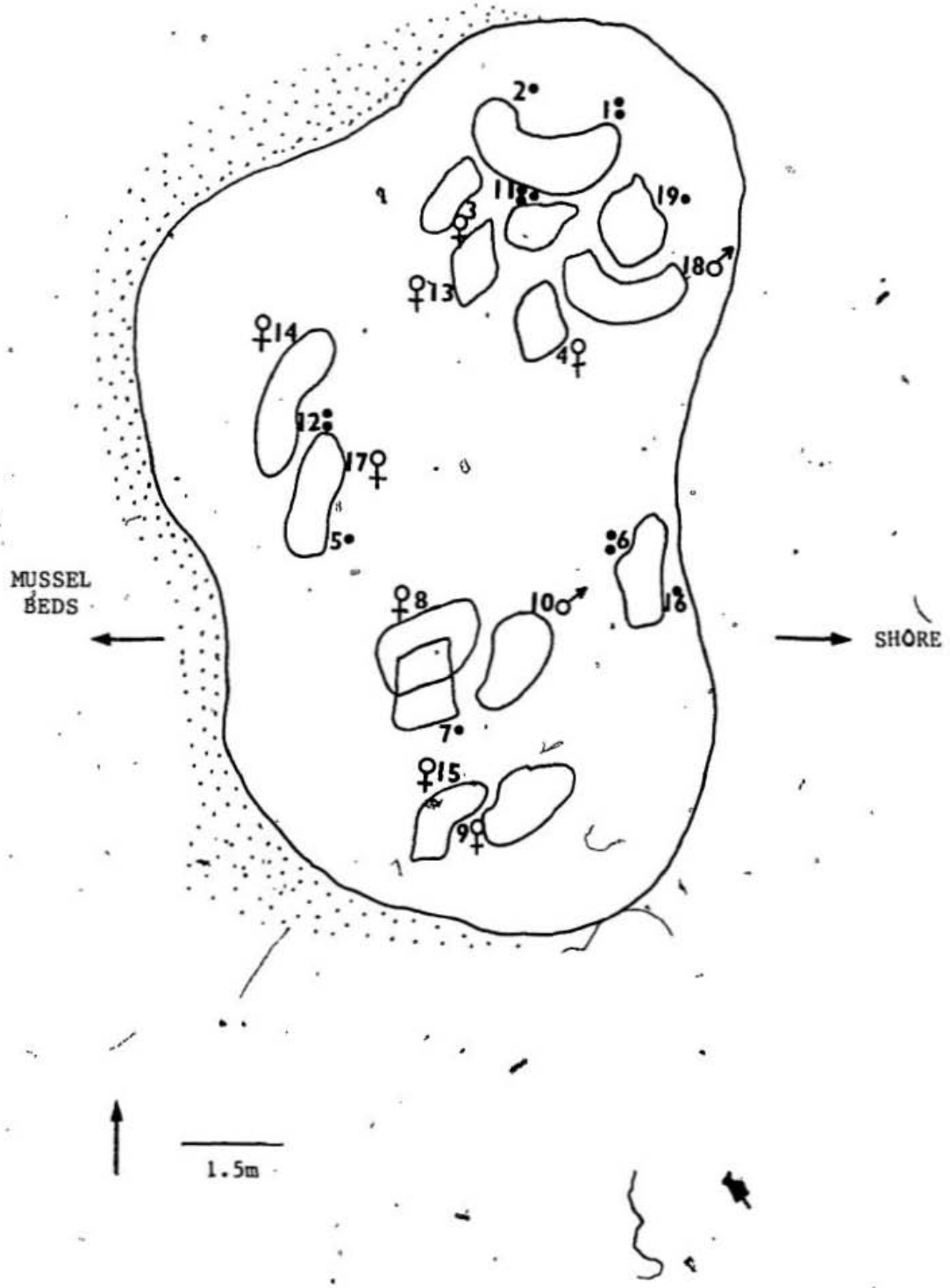

6
7
5
4
11
8
13
9
18
19
10
17
2
3
20
23
14
21
12
15
16
22
1
MUSSEL BEDS
SHORE
1.5m

Figure 8: Bellevue, Trinity Bay, transect site 1987. Symbols identical as those found in Figure 7.



32 (b)

crevice sites. In addition, positions chosen as crevice sites did not appear to change from year to year. It is unknown whether individuals re-established the same home crevices from year to year since identification of individuals was not possible year-to-year. Some individuals definitely do not return to the same crevice, as the sexes of inhabitants were not the same between years. Juvenile 'shannies were not found in the same area between dives, and were presumed not to be territorial.

Individuals which were tagged in August 1986 remained on the transect until November 1986. However, no tagged individuals were found on the transect in the 1987.

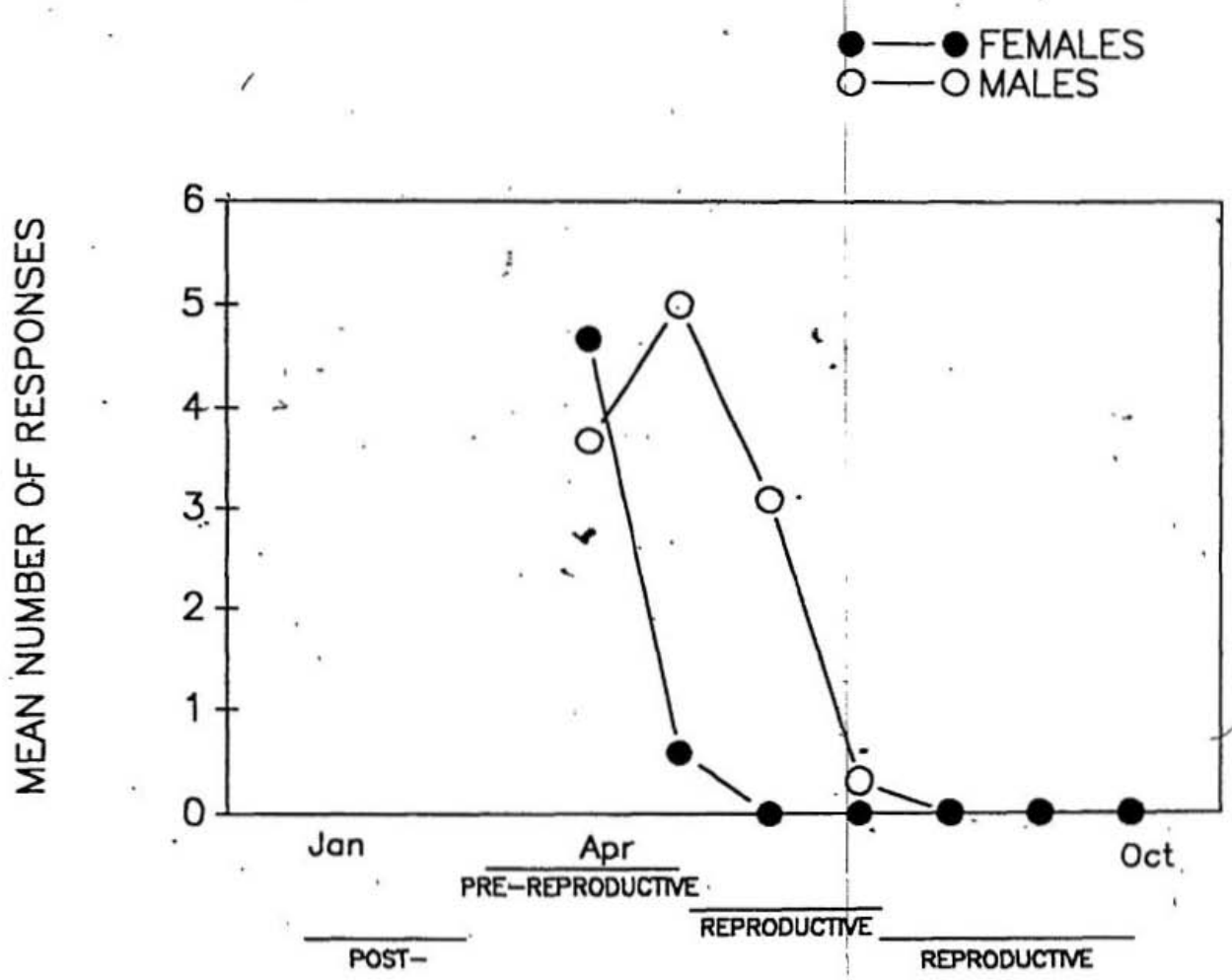
Activity-level counts revealed fish activity was affected by tidal cycle and time of day (contingency table $X^2 = 6.42$, df=3, $p < 0.05$; data: Appendix 4). More fish were seen during dusk dives at high tide, than dusk dives at low tide or afternoon dives at high or low tide. Activity-level counts were not significantly different between the three reproductive periods ($F=1.21$, df=1,2, $p=0.361$). However, this result may be confounded by the fact that counts were only done during day or dusk, and no counts were performed from November to April when fish were not present on the transect.

Males were significantly more aggressive than females in response to the model in both mean distance of response and the mean number of responses to the model intruder (t-

test; t=11.56, df=1, p<0.05; t=5.84, df=1, p<0.05). Females stopped responding to the model when reproductively spent (Figure 9 and 10). Male response to the model decreased late in the season when their eggs disappeared (presumably hatched; Figures 9 and 10). There was a significant difference between the three reproductive periods in number of the responses to the model (F=345.84, df=1,2, p<0.01), and the distance of response to the model (F=65.43, df=1,2, p<0.01). The reproductive period had the highest values for both variables and for both sexes. Both males and females increased their aggression during the pre-reproductive period after returning to the study site. Peak female aggression occurred at the onset of the reproductive period and decreased abruptly after spawning. Male aggression peaked later in the reproductive period during egg guarding. Male aggression increased as time spent guarding eggs increased. Among males, non-reproductive males were significantly less aggressive throughout the year than reproductive males in response to the model (t=14.70, df=1, p<0.05).

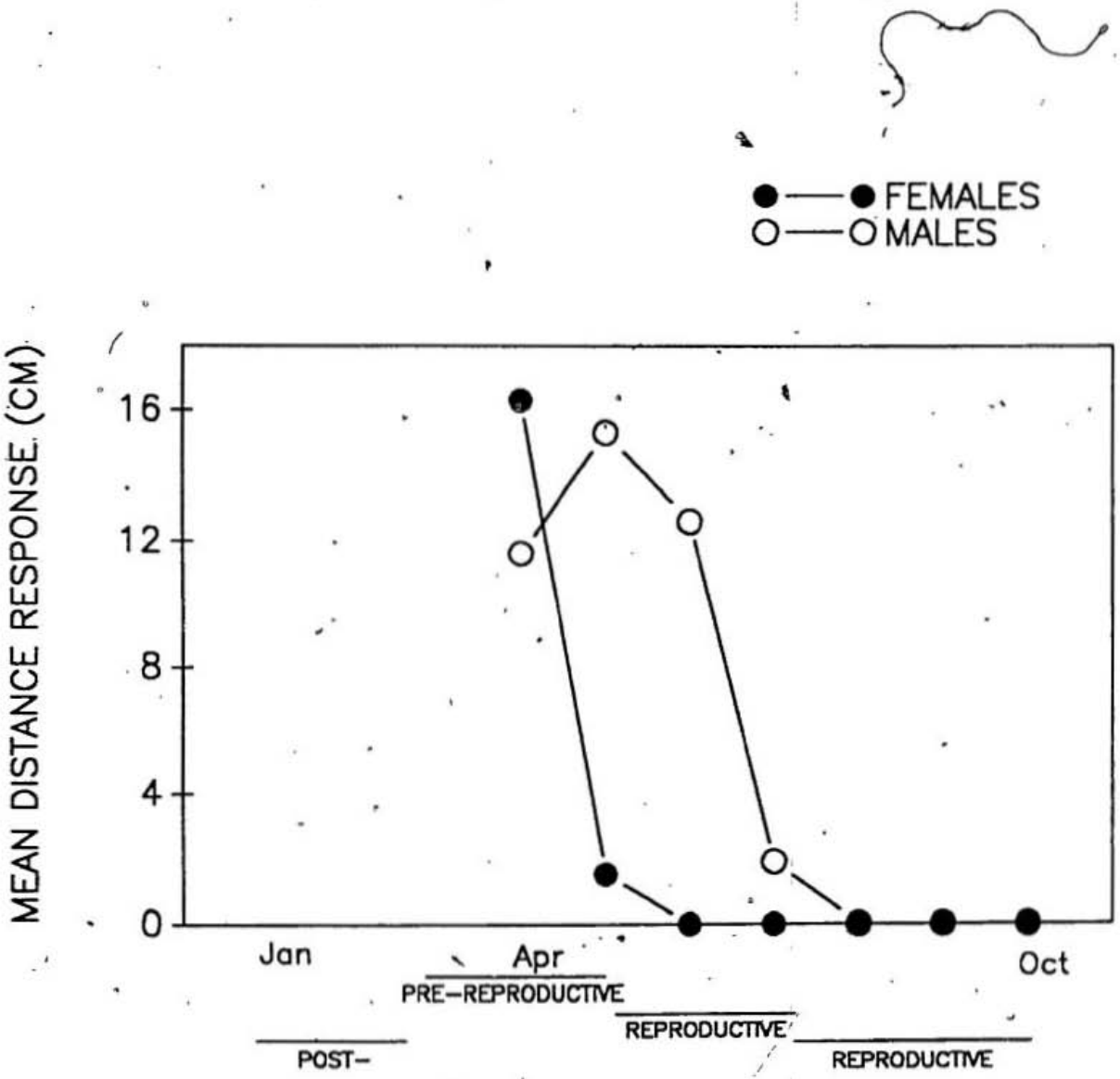
Within the six introductions of the model during the weekly presentations, the first two introductions elicited a significantly greater mean distance of response than the last two introductions (t= 8.34, df=1. p<0.05). Hence, it appears habituation did occur during a presentation series.

Figure 9: Mean number of responses to male model intruder by fish on field study site over one year. Year represented as in Figure 2.


FEMALES
MALES
MEAN NUMBER OF RESPONSES
6
5
4
3
2
1
0
Jan
Apr
Oct
PRE-REPRODUCTIVE
REPRODUCTIVE
POST-
REPRODUCTIVE

35 (b)

Figure 10: Mean distance response to male model intruder by fish on field study site over one year. Year represented as in Figure 2.


FEMALES
MALES
MEAN DISTANCE RESPONSE (CM)
16
12
8
4
0
Jan
Apr
Oct
PRE-REPRODUCTIVE
REPRODUCTIVE
POST-
REPRODUCTIVE

36 (b)

However, habituation did not increase from week to week as the mean distance of response of males peaked at the onset of the reproductive period, a month after the model presentations (Figure 10). In addition, patterns of response to the model were different between the sexes (Figure 10). If habituation had occurred there should have been a steady decline in mean distance of response for both sexes.

1.4. DISCUSSION

Territoriality is exclusive use of space by one individual (Kaufman , 1983). Active defense and overt aggression may be necessary for establishment, but not necessary for maintenance of a territory (Kaufman 1983). Results of this study demonstrate that at Bellevue, Trinity Bay, Newfoundland, adult Ulvaria subbifurcata, have exclusive use of a crevice site which is actively defended from late March to early November. In the laboratory, each fish maintained exclusive use of a crevice site for 12 months, with no crevice sharing or switching. Hence, the crevice site can be considered a territory. Single burrow territories have also been noted for the mudskipper, Periophthalmus sobrinus (Magnus 1972). From field and laboratory observations, it appears a home range exists around the crevice site which is not exclusively used by one fish. Thus, the use of space by U. subbifurcata involves a combination of territoriality and space sharing. The phenomenon of peripheral space overlap has been reported in other territorial fishes, including Abudefduf zonatus (Keenleyside 1972), Hypoplectrus spp. (Barlow 1975), and Sebastes spp. (Larson 1980).

In November, shannies at Bellevue, Newfoundland, leave their crevice sites. No fish were observed on the Bellevue study site during the winter dives (November- April), and

presumably fish move offshore to ice-free areas. It should be noted that offshore refers to short distances from shore in slightly deeper water. Several other fish species migrate offshore presumably for food resources (Newell 1979), thermal preference (Hestagen 1979), or ice-free habitats (Gibson 1986). The offshore migrations noted in this study may be a field site anomaly. LeDrew and Green (1975) were able to collect mature adults during winter months in other inshore bays in Newfoundland. Because of the shallow depth of the channel at Bellevue, ice may be a problem during winter months (pers. obs.; D. Methven, pers. comm.). In fact, the study site during winter dives was barren of all fish (pers. obs.).

While offshore, space usage of U. subbifurcata is unknown. Generally, little is known about offshore activity of fishes during the winter months (Gibson 1986; except Fisher 1975), which is a result of the difficulty of field work done during winter. During the time of offshore migration, laboratory-held fish maintained a crevice site. However, aggression was extremely low. If territories/ crevice sites were not maintained in the wild during these winter months one would expect a diminished amount of exclusive use of space in the laboratory during this time. This did not occur. Nevertheless, laboratory-held fish were collected from Portugal Cove, Newfoundland, an area where migration has not been determined.

Why does U. subbifurcata need a territory? It appears that at Bellevue, territoriality is needed for shelter for females and males, and spawning and egg guarding for males. Other temperate marine fishes that exhibit seasonal territoriality, associated with reproduction, are Porichthys porosissimus (Moore 1970) and Hypsoblennius spp. (Stephens et al. 1970). However, if territoriality is maintained year-round in a seasonal spawner, territoriality cannot solely be for reproduction. The function normally ascribed to non-reproductive territoriality is partitioning of environmental variables, such as shelter or food, to ensure efficient use of resources (Gibson 1982). Access to shelter is especially important for small intertidal fish which are incapable of sustained swimming. They can best avoid capture by predators by entering holes and crevices (Gibson 1982). In fact, in Chasmodes bosquianus, dominant individuals, which have greater access to crevice sites than do subordinate individuals, escape predator attacks more frequently than do subordinate individuals (Phillips and Swears 1979). In the radiated shanny it is unclear whether the territory functions as a feeding territory. However, the manner in which the fish feeds suggests that territoriality is unnecessary for food acquisition. The shanny bites at food within its crevice and also, actively swims outside of its crevice (territory), biting food (pers. obs.). In summary, territoriality in U. subbifurcata might

be maintained for reproduction and shelter.

As stated previously, aggression is necessary for territorial establishment, but is rarely necessary for maintenance of a territory (Kaufman 1983). Generally, social spacing in nature is in a state of dynamic equilibrium and aggressive behaviour and territorial disputes are minimal. Miles (1974) showed the rate of aggressive activity can increase when the existing social structure of mudskippers was altered by introducing a new fish. If territory maintenance was the sole function of aggressiveness in U. subbifurcata, one would have expected an increase in aggression when migrating fish re-establish territories during spring, or when fish were introduced in a laboratory aquaria. However, aggression in Ulvaria subbifurcata began to increase during the pre-reproductive period (March - April) and peaked during the reproductive period (May - June) for both males and females. Hence, aggression peaks later in the season in the field than would be expected for territory re-establishment. Furthermore, peaks in aggression in laboratory-held fish were observed when no individuals were introduced. Increases in aggression, other than territory dynamics, have been attributed to temperature (e.g. Fitzgerald et al. 1986), density (e.g. Stanley and Wootton 1986), and reproduction (e.g. Davies 1978). Temperature alone cannot explain the levels of aggression in this present study. The same sea

temperatures are found during spring and fall, and the pre- and post-reproductive periods corresponding to similar sea temperatures (approximately 4.0°), show very different levels of aggression. Density cannot explain the increase in aggression in the laboratory or the field since density in laboratory was held constant and density of shannies on the transect was constant from year to year. It appears that aggression is linked with the reproductive cycle of the fish. During the pre-reproductive period, individuals in the field are returning inshore and establishing territories. A proportion of the increase in aggression could be attributed to territory establishment. However, the fact that the increase is also recorded in the laboratory suggests that increased GSI and hormonal levels during the reproductive period could be a proximate cause for the increase in aggression.

Other evidence for the link of aggression to the reproductive period is the change in male aggression towards females from the non-reproductive season to the reproductive period. Males reduce the number of aggressive encounters with females while increasing the number of encounters with other males. This suggests male/male competition at the time of reproduction. During this period, females are increasing the number of encounters with males. Because it is the female that searches for a mate, a female may have to increase aggression during her time outside the crevice.

The cost of increased aggression and searching for mates is attributed to higher mortality in females in the beaugregory damselfish (Itzkowitz 1985).

Several other characteristics of aggression in U. subbifurcata support the association of aggression to reproduction. Males are more aggressive than females throughout the year. However, this difference is greatest during the pre- and the reproductive periods. Males engage in encounters which are more intense, longer, and in greater frequency than those of females. Interestingly, outside the reproductive period males show more aggression to females than females show to males. If aggression was not associated with reproduction one would expect the sexes to be equal in aggression levels since the value of the shelter should be equivalent for both. The fact that males are more aggressive than females has been noted in several other fish species (e.g. beaugregory damselfish; Itzkowitz 1985; lumpfish; Goulet et al. 1986).

When examining aggression levels in the reproductive period, female aggression reaches a peak at the very end of pre-reproductive period and the beginning of the reproductive period. Females cease being aggressive after spawning (mid-May). However, male aggression peaks at the onset of the reproductive period and dramatically falls off when eggs have hatched, several weeks after females have ceased being aggressive. This peak may indicate the end of

the reproductive phase and the start of the parental phase of the reproductive period. Males need to be aggressive during the parental care phase of the reproductive period in order to guard against egg predators (Gross and MacMillian 1981; Bain and Helfrich 1983). However, it is also not advantageous to be too aggressive as circumstantial evidence exists for detrimental effects of high levels of male aggression on the quality and quantity of parental care, and subsequent hatching success of eggs (Van den Assem 1967; Sargent and Gebler 1983; Sargent 1985).

Another characteristic pattern of male shanny aggression occurs at the time of parental care. As time spent with the eggs increases male aggression decreases. This is in contradiction to Sargent and Gross (1977) and Colgan and Brown (1988) who state that nest defense intensity is directly related to time spent guarding eggs, since the value of the eggs increases as investment increases. However, Knight and Temple (1986) contend that increases in nest defense through the nesting cycle found in several avian and fish studies are largely methodological artifacts. They suggest that when an observer repeatedly visits or brings a potential predator to a nest and records the parent responses, the nest-defense behaviour is gradually modified by positive reinforcement and fear reduction. That is, after being approached, the potential nest predator leaves without harming the nest, fear is

reduced, and response to the potential predator increases. Although a nest predator was introduced in this manner for this study, habituation appeared to occur during a set of six presentations, but not from week to week. In this study, aggression was indirectly related to time spent with the nest.

In summary, this study demonstrated U. subbifurcata at Bellevue, Trinity Bay, holds a territory from March to October. The territory is surrounded by a home range. It appears the territory is for shelter and reproduction. During November to March, U. subbifurcata found at Bellevue, Trinity Bay, Newfoundland, probably move offshore to ice-free areas. Finally, the observed pattern of aggression appears to be associated with both territory establishment and reproduction.

CHAPTER 2 MATE CHOICE

2.1. Introduction

Halliday (1983) defines mate choice as any pattern of behaviour shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others. The benefits that animals may derive by choosing a particular mate over another range from immediate gains such as courtship feeding to the longer term advantage of mating with an individual of high genetic quality (Partridge and Halliday 1984).

In species where females are the choosier sex and males neither defend resources nor provide parental care, females should be interested in sexual competence, as measured by fertilization efficiency (e.g. Davies and Halliday 1977) or sperm supply (Trivers 1972; Nakatsuru and Kramer 1982). In addition to sexual competence, females should also select for "good" male genes as expressed by the ability to live longer than others (e.g. Trivers 1972), the ability to grow large (e.g. Gandolfi 1971), or the ability to be dominant among other males (i.e. Cox and Leboeuf 1977). Longevity, growth, and dominance are not necessarily mutually exclusive characteristics and are often difficult to separate. In addition, although females choose mates with these characteristics, the traits are not genetically "driven" by sexual selection, but rather by natural selection.

When males provide resources females should be influenced by the qualities of the resource and the defending male (Emlen and Oring 1977). Females may select for nest sites (e.g. Zimmerman 1971; Kodric-Brown 1977; Itzkowitz 1978), food (e.g. Verner and Willson 1966; Thornhill 1976; Gwynne 1984), refuge (e.g. Searcy 1979; Borgia 1981), or parental ability (e.g. Nisbet 1973; Grant and Colgan 1983).

Studies of mate choice and reproductive success in marine fish have focused on broadcast spawners that defend temporary spawning sites and show no parental care (e.g. Warner et al. 1975; Warner and Robertson 1978; Jones 1981). Among territorial egg-guarders, Schmale (1981) demonstrated that mating was non-random in the bicolour damselfish Eupomacentrus partitus, and that male mating success correlated with total length, inter- and intra-specific aggression, and courtship frequency. Thresher and Moyer (1983) found that male reproductive success correlated with male size in the damselfish Glyphidodentops cyaneus and E. partitus, but not in Pomacentrus wardi, G. rollandi nor G. bioullotus. Information on mating systems of temperate fish species is scarce. Reproduction is seasonal and short-term in temperate marine species, and this can affect selective pressures on temperate animals. Cole et al. (1986) found that in the temperate marine goby, Coryphopterus nicholsi, females preferentially spawn with

males which court most vigorously. Cole found no correlation between territory quality and spawning success. Goulet et al. (1985) found no mating preference in the lumpfish, Cyclopterus lumpus, although males guard and aerate eggs. None of these studies have investigated the mechanisms of choice.

Ulvaria subbifurcata, a temperate marine stichaeid, offered an excellent opportunity to examine female choice and its mechanisms. Female U. subbifurcata deposit eggs in male nest sites where they are guarded and aerated by the males until they hatch as planktonic larvae (LeDrew and Green 1975). Females are monogamous, while males are polygynous. Monogamy, in this context, is defined as spawning once and only with one male during the reproductive season. It is common to find mature males in the wild with various numbers of egg masses each in their single crevice site (LeDrew and Green 1975). Hence, female mate choice appears to occur since a lack of choice would result in a random distribution of egg masses when sex ratios are equal.

Since the male radiated shanny provides a resource, a nest site, and care of the eggs, female choice is expected to be based on either the qualities of the nest and/or the male (Emlen and Oring 1977). Preliminary observations indicated male nest sites to be similar qualitatively and quantitatively. In addition, in the previous section of

this study it was found that adult shannies probably migrate offshore during winter and return inshore to spawning areas in spring. Thus, return appearance to spawning areas may indicate male quality and subsequently, play an important role in male spawning success. Using both laboratory and field observations I addressed the following questions: 1) Is female choice influenced by the quality of the male (size, aggression, or prior residency)?; and 2) What are the mechanisms of female choice?

2.2. Methods

2.2.1. Laboratory Experiments

Three experiments were performed during May - July 1986 and 1987 to examine the influences of male size, male aggression, and male prior residency on female choice.

General Protocol

All fish were collected by SCUBA in April and May 1986 and 1987 from Portugal Cove, Newfoundland. Prior to testing all males and females were kept in a holding aquarium (90 X 70 X 40 cm; 252 l) with water temperature maintained at 3.0-4.0°C. Males and females were separated in the aquarium by a mesh partition to avoid any male/female physical interaction before testing.

The experiments were performed in two aquaria of equal size (150 X 100 X 80 cm; 1200 l). Both the holding and experimental aquaria were placed in a blackened room with reversed photoperiod (see Section 1.2.1.). Dusk and dawn (1 hour each) were simulated by a 25W frosted bulb, located centrally above each aquarium. Day was simulated by two 60W florescent tubes, located on the ceiling of the room. Three 25W red bulbs evenly placed above each of the aquarium enabled observations to be made during the simulated dark hours (See section 1.2.1.). Each experimental aquarium was covered on four sides with black plastic to minimize

external light and observer disturbance with three flaps one side to permit observations. Substrate and crevice sites were identical to those described in Section 1.2.1. except each aquarium contained 3 crevice sites. Observations of fish in the experimental aquaria were made for 1 hr between 0900 and 1200 and between 1400 and 1700. The first observation period during the reversed photoperiod (0900 - 1200) was chosen because it is the initial period of simulated darkness and activity. In addition, spawning has been shown to occur during dim periods in the laboratory (Green et al. 1988). The second recording session (1400-1700) was chosen because it corresponds to midnight - 2 am, which Goff and Green (1978) found to be a period of peak activity in the field. In each experiment the all-occurrence technique was used (Lehner 1979).

At dusk of day 1, three males were selected from the holding aquarium and introduced into each experimental aquarium. Initial responses of the males and their movement in the aquarium during 30 min by each male was noted. Males were allowed to acclimatize for 24 hr before twice daily observations began. Water temperature and initial positioning of each male within the aquarium was noted at the onset of each recording session. During each session all aggressive encounters were described as in Section 1.2.1., with the addition of maximum distance which elicited an aggressive response.

On day 3, a gravid female from the holding aquarium was selected, measured (total length) and introduced into the observation aquarium at dusk. Initial female and male responses were recorded. Observations were performed for 1 hr between 0900 and 1200 and between 1400 and 1700. Male/male interactions and female/male encounters were recorded as well as the number and duration of female visits to males and their nest sites, and the males' responses to the visits. A visit was defined as the presence of the female in a male's nest site for at least 10 sec. This protocol was followed until the female spawned or until five days had elapsed. If a spawning occurred during the observation period, the duration of the spawning, the spawning partner, and all spawning activities were described. After spawning the female and eggs were removed from the aquarium. Egg volume was determined by measuring the length, width, and depth of the mass (see field observations 2.2.2.). The numbers of eggs were also counted. All males were removed from the aquarium and measured (total length). All nest sites were removed and scrubbed and the gravel thoroughly mixed to remove any 'spawning scents' to minimize any pheromonal bias for the next run of an experiment. If no spawning occurred the female was removed and placed in a separate holding tank and not used again for any choice experiments. The males and nests were treated in the same manner as when a spawning

occurred. Three males were used for three runs of an experiment.

Experiment 1

This experiment tested the prediction that male size influences female choice. Three males of different size classes, small (9.0 - 10.0 cm), medium (10.5 - 11.5 cm), and large (>12.0 cm), were placed in an experimental aquarium containing three similar sized and positioned nest sites; thus nest quality was held constant. Each crevice was positioned in the aquarium so that one side of the crevice was adjacent to an aquarium wall. Intensity and duration of all aggressive encounters were recorded before and after the introduction of the female. Male size was compared to spawning success. Aggression parameters were then analyzed between successful (individuals that spawned) and unsuccessful males (individuals that did not spawn) using a nonparametric Mann Whitney test. In addition, number and durations of female visits were compared between successful and unsuccessful males using a nonparametric Mann Whitney test. A Mann Whitney test was used since males were categorized as successful (1) or unsuccessful (0). Level of significance was 0.05.

Experiment 2

This experiment tested the prediction that male behaviour (aggression) influenced female choice. Three

males of similar length (± 0.2 cm) were placed in an aquarium containing three similar-sized and positioned crevices; thus, male size and nest quality were held constant (similar crevices as described in experiment 1). Male/male and male/female interactions were recorded as in experiment 1. Statistical analyses were as previously described for experiment 1.

Experiment 3

This experiment tested the prediction that prior residency influenced female choice. One male was placed in the aquarium 48 hours prior to the introduction of the remaining two similarly-sized males (± 0.2cm). Each male had one opportunity to be the prior resident in a total of three runs. Similar crevices or nest sites were available to the males (as previously described). Statistical analyses were as previously described for in experiment 1. In addition, nest acquisition with respect to male prior residency was examined.

2.2.2. Field Observations

At least once per week during late April, May, and June 1986 and 1987, the Bellevue transect was searched at dusk for the presence of fish and egg masses. If an egg

mass was found an estimate of egg number was obtained; (from lab experiments a regression of egg mass volume and egg number was used to extrapolate field egg number from egg volume). Male spawning success was determined by the number of egg batches, the number of eggs, and the temporal appearance of egg batches. These were then correlated with male size, crevice substrate, and fish appearance on the transect.

In order to test the prediction that the most aggressive males would receive the most matings, a presentation experiment was performed. A model male intruder was constructed (previously described in Section 1.2.2.) and was presented to five males on the transect at Bellevue during the pre-reproductive, the reproductive, and the post-reproductive periods (as defined in section 1.2.1.). The number of responses and the mean distance of the response to the model were correlated with male size. The presentation was always made during the late afternoon or dusk to eliminate daily variation in responses. In both laboratory and field observations, male aggression, size, activity, and prior residency were compared with male spawning success.

2.3. RESULTS

Before presenting the results of the mate choice experiments four observational, non-quantifiable points should be mentioned. Firstly, when gravid females were introduced into an aquarium with the three males, no immediate aggression was observed. No male/female aggressive encounters were observed. When females approached and entered nest sites; no aggressive postures were displayed by either sex. Only male/male aggressive encounters were observed.

Secondly, on only one occasion was spawning observed. On all other occasions (16), spawning occurred at dawn or dusk when observations were not performed. In the observed spawning, both the male and the female participated in abdomen and gonadalpore rubbing (Green et al. 1988; pers. obs.). Once the eggs were extruded by the female, the male proceeded to wrap his body around the eggs to form the eggs into a compact mass.

Thirdly, in the prior residency experiment, no exchange of nest sites occurred regardless of which individual was the prior resident. This should have been expected since nest site quality was held constant. Hence, no nest site bias was apparent.

Fourthly, in the field, all adults were found among the boulders. Only juvenile shannies were found among the

pebbles, small rocks, and mussel shells. There appeared to be no substrate quality difference among the adults.

2.3.1. Laboratory Observations

The three mate choice experiments were performed during the 1986 and 1987 reproductive seasons. Each experiment consisted of trials which were observations on three males and one introduced female and runs which consisted of several trials with the same three males used in each trial. Seventeen spawnings occurred during the experiments. A summary of all fish used in each trial in all runs for all three experiments is found in Appendix 5. For statistical purposes all trials of each experiment were combined and comparisons were made between successful males (those which spawned) and unsuccessful males. Discrete classification of males was possible since one male in all trials of a run received all the spawnings in all experiments. It should be noted that female size, relative to male size, could not be controlled since it was necessary to select the most gravid female for each trial to maximize the number of runs and trials in a reproductive season.

Experiment 1

In this experiment a total of six males and five females were tested. The largest male in each run received

all six spawnings (3 and 2 each). These successful males had significantly more aggressive encounters (Mann Whitney; U= 21.5, df= 1,2, $p<0.05$; Figure 11) which were longer (U= 31.5, df= 1,2, $p<0.05$; Figure 12), and more intense (U= 30.5, df= 1,2, $p<0.05$; Figure 13) than the four unsuccessful males. Successful males also had a significantly greater maximum distance of response (U= 21.5, df= 1,2, $p<0.05$; Figure 14), and spent significantly more time out of their crevices (U= 13.0, df= 1,2, $p<0.05$; Figure 15) than unsuccessful males.

In all trials the introduced female visited each experimental male at least once before spawning. However, successful males received significantly more and longer visits by the female than unsuccessful males (U= 36.5, df=1,2, $p<0.05$; U= 46.4, df= 1,2, $p<0.05$; Figure 16 and 17, respectively). Thus, the female visited most often and for longer periods of time, the male with whom she eventually spawned. The results for this experiment were so consistent and conclusive that only two runs were performed.

Experiment 2

In this experiment a total of 9 males and 9 females were tested. Three runs were performed because the differences in the levels of aggression among males was not as distinct as in the previous experiment. Also, during six of the eight trials performed, four to five days elapsed

Figure 11: Successful vs unsuccessful males in the mean number of aggressive encounters per observation period in all three laboratory experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.

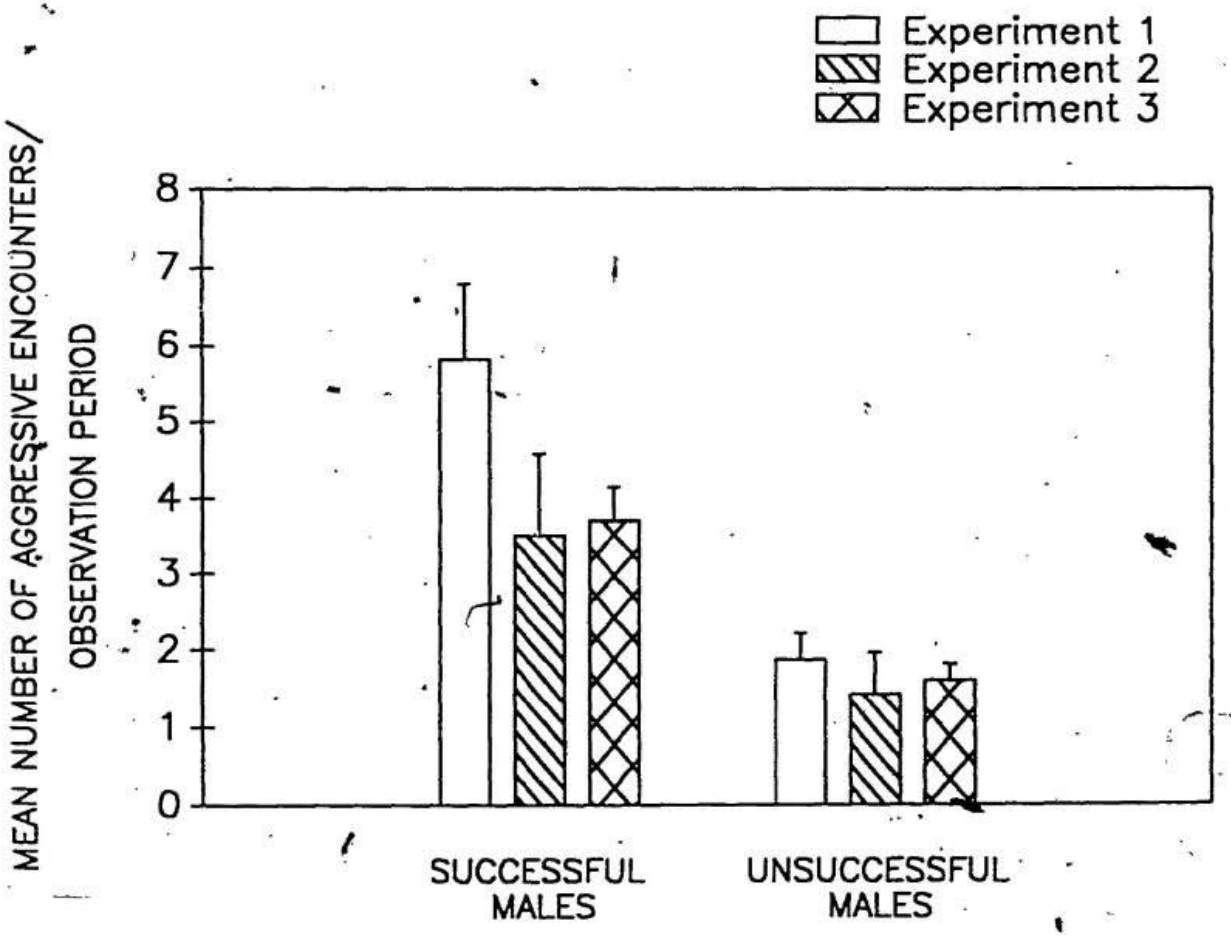
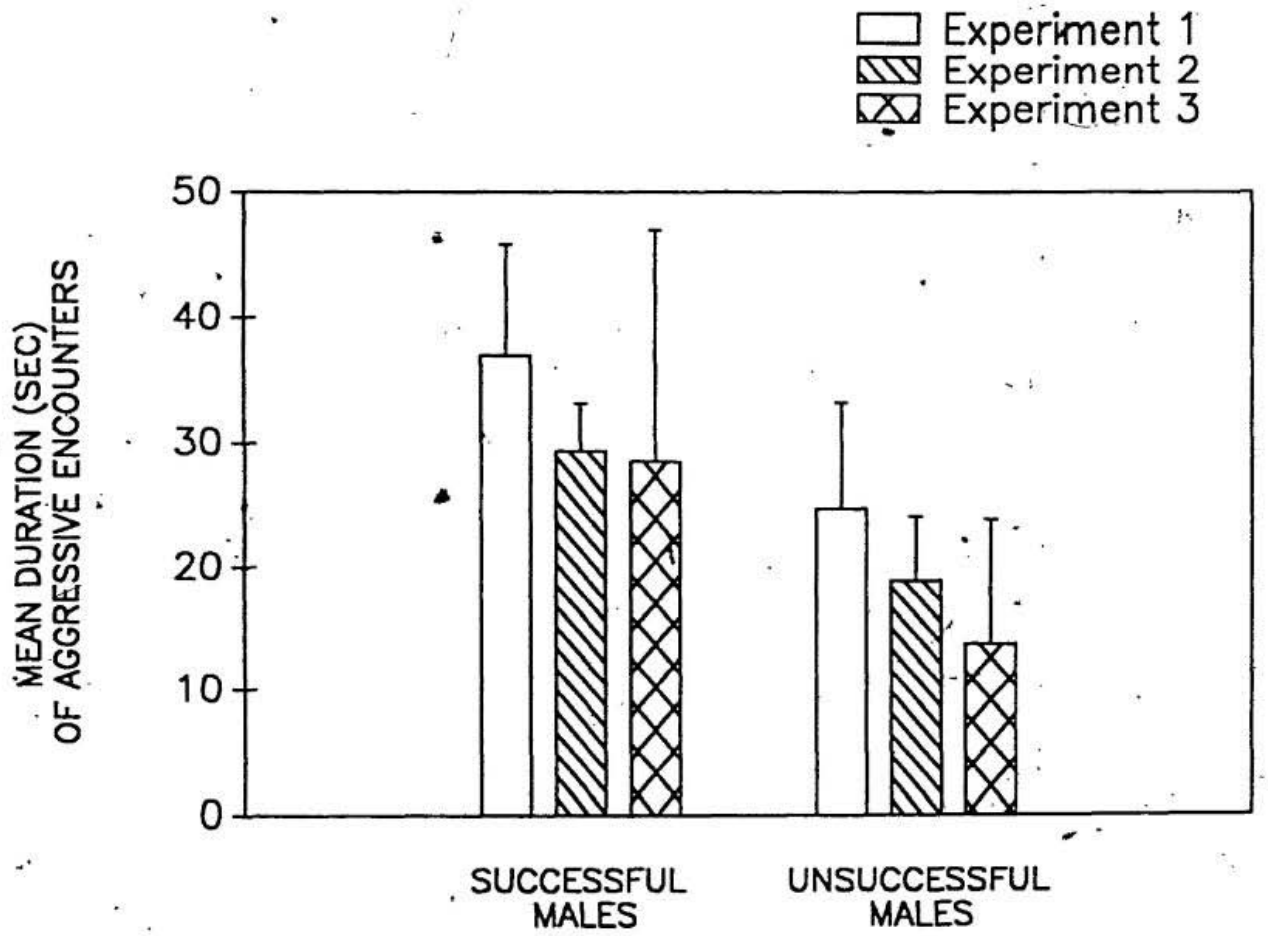
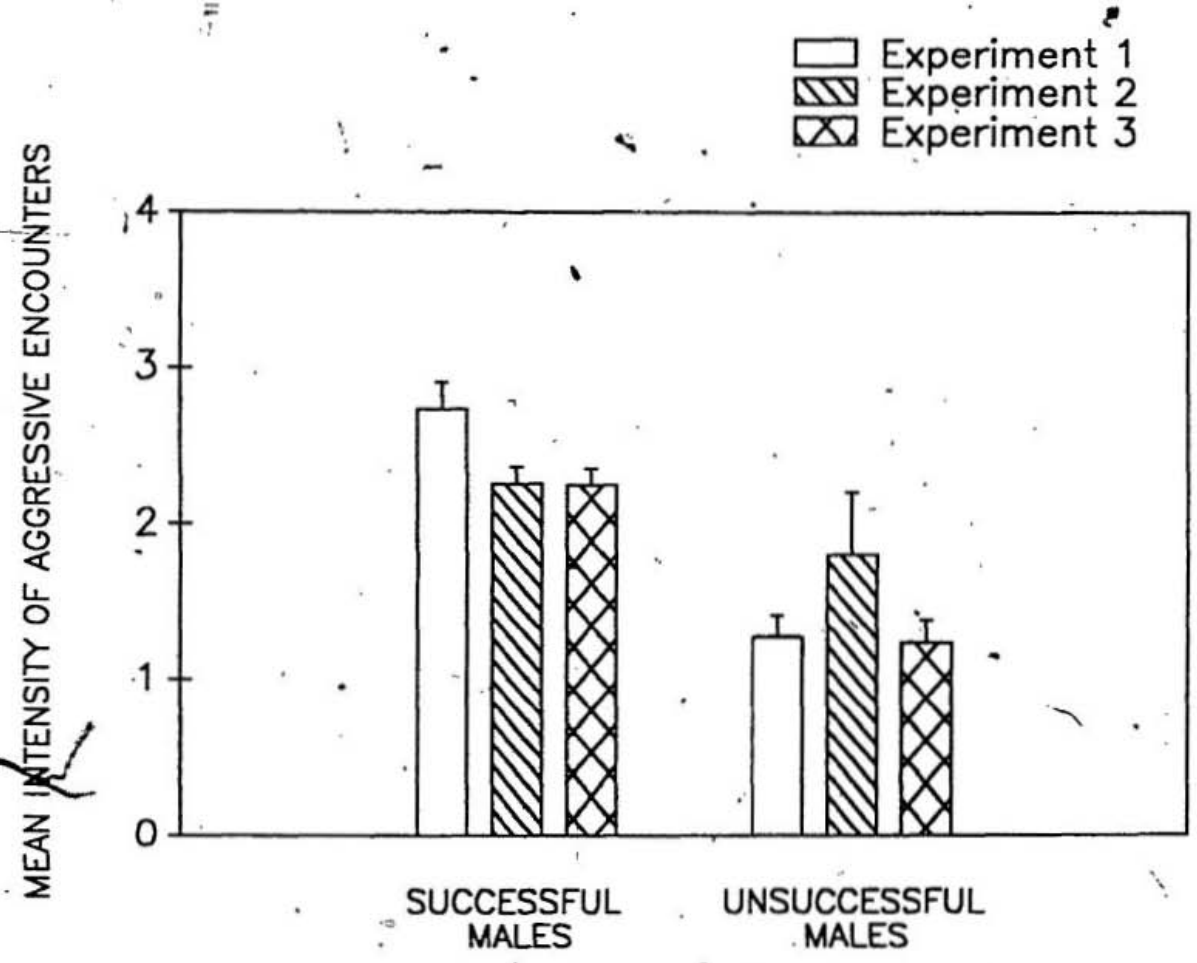

Experiment 1
Experiment 2
Experiment 3
MEAN NUMBER OF AGGRESSIVE ENCOUNTERS/ OBSERVATION PERIOD
0
1
2
3
4
5
6
7
8
SUCCESSFUL MALES
UNSUCCESSFUL MALES

Figure 12: Successful vs unsuccessful males in the mean duration (sec) of aggressive encounters of all three laboratory experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.


Experiment 1
Experiment 2
Experiment 3
MEAN DURATION (SEC)
OF AGGRESSIVE ENCOUNTERS
50
40
30
20
10
0
SUCCESSFUL
MALES
UNSUCCESSFUL
MALES

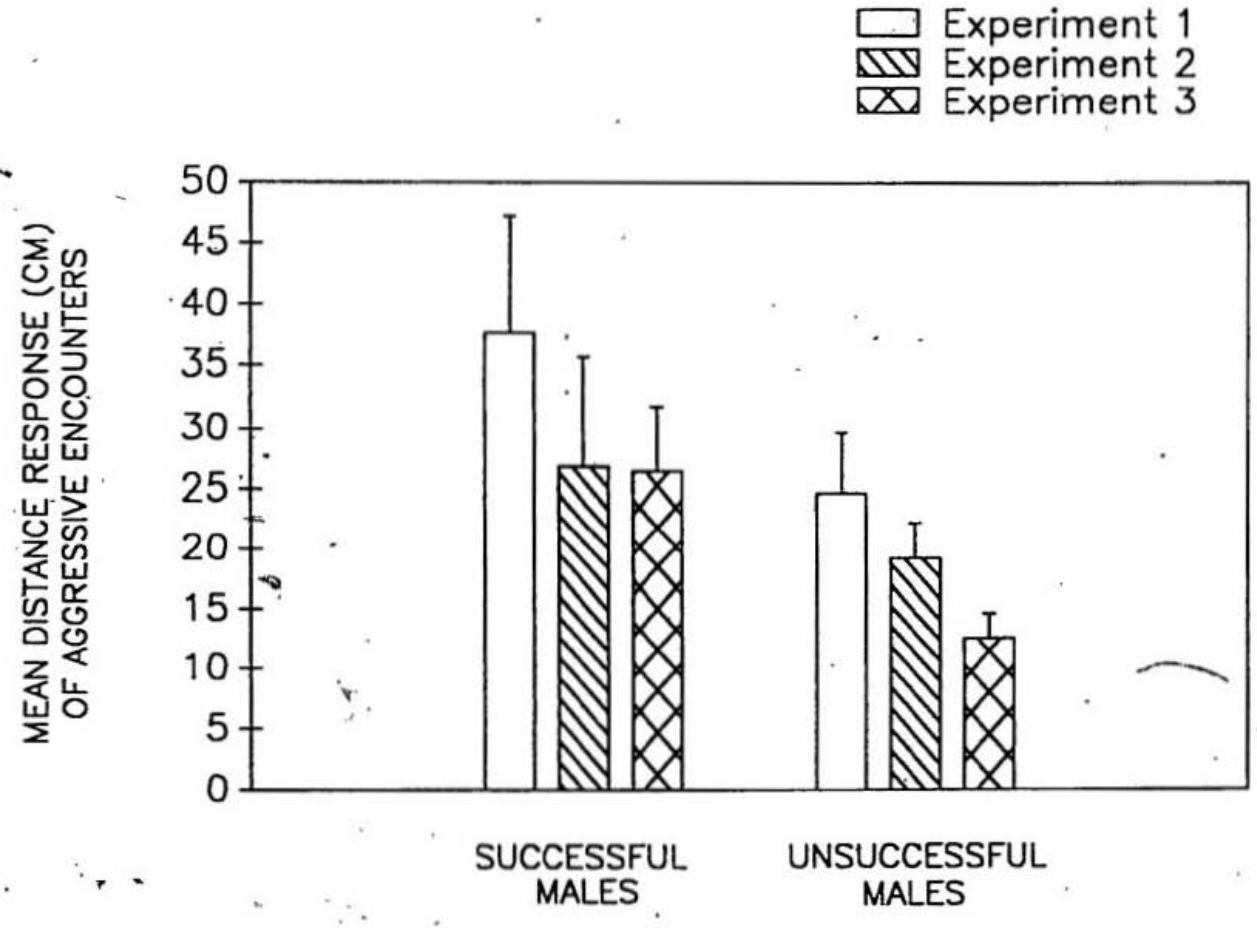
(q) 09

Figure 13: Successful vs unsuccessful males in the mean intensity of aggressive encounters in all three experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.


Experiment 1
Experiment 2
Experiment 3
MEAN INTENSITY OF AGGRESSIVE ENCOUNTERS
0
1
2
3
4
SUCCESSFUL MALES
UNSUCCESSFUL MALES

(q) 19

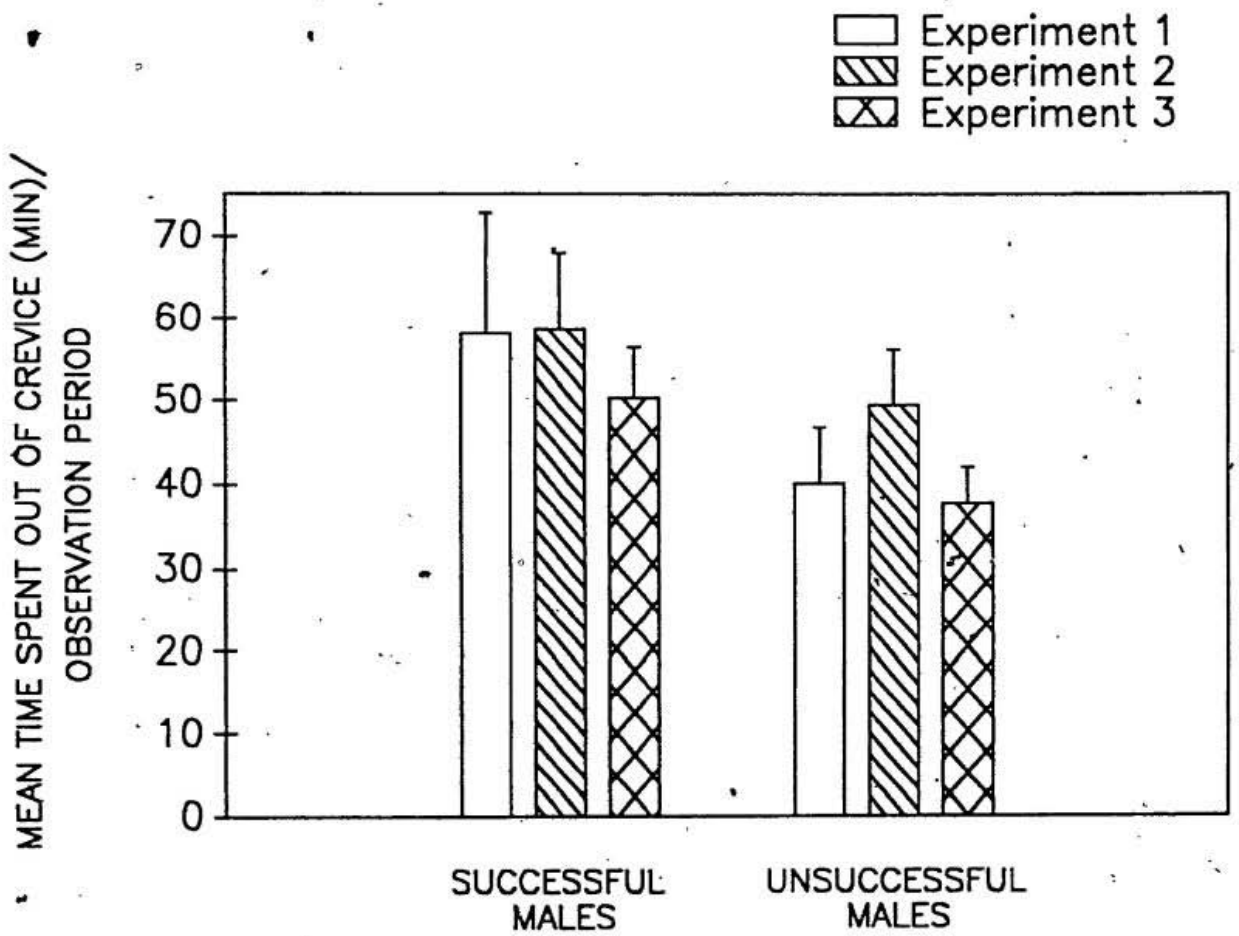
Figure 14: Successful vs unsuccessful males in the mean distance response per aggressive encounter in all three laboratory experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.


Experiment 1
Experiment 2
Experiment 3
MEAN DISTANCE RESPONSE (CM)
OF AGGRESSIVE ENCOUNTERS
50
45
40
35
30
25
20
15
10
5
0
SUCCESSFUL
MALES
UNSUCCESSFUL
MALES

(9) 29

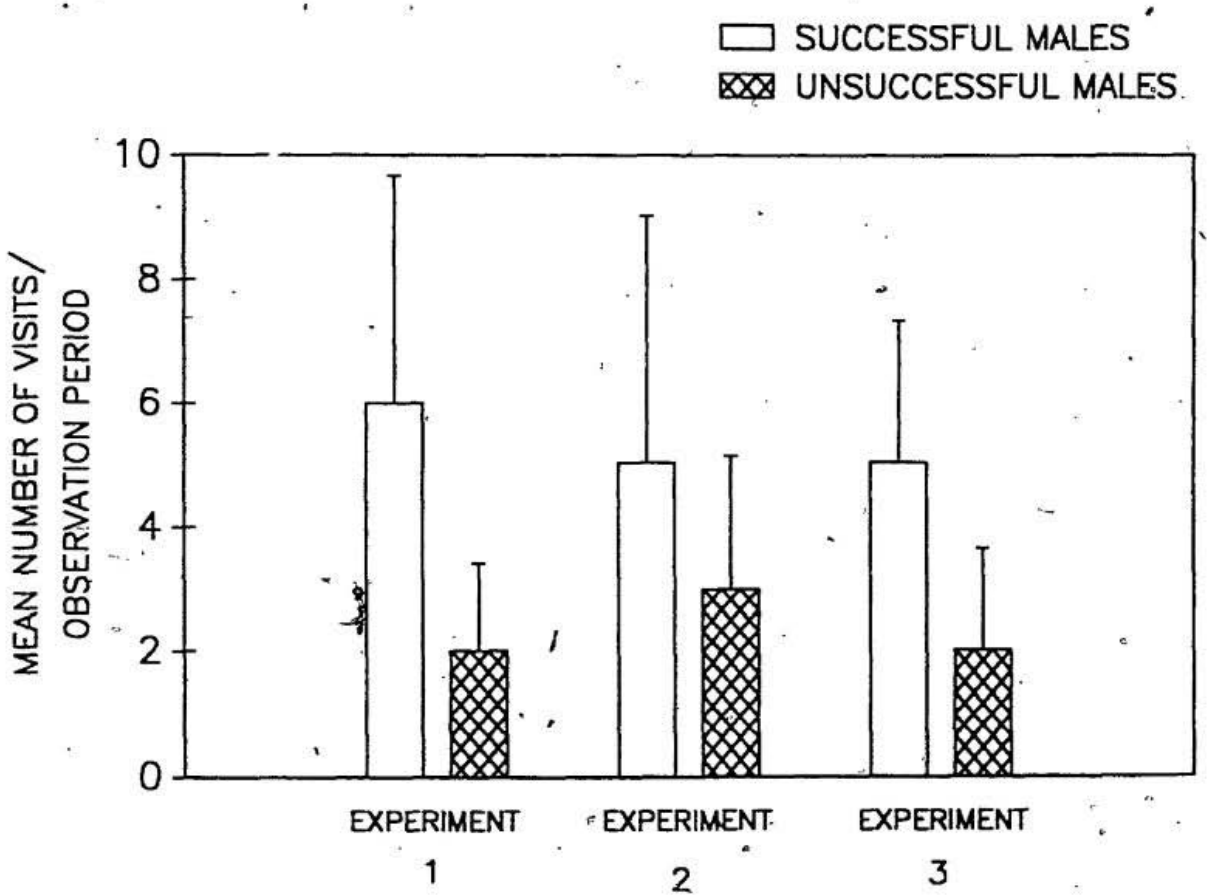
62 (b)

Figure 15: Successful vs unsuccessful males in the mean time spent out of crevice sites per observation period in all three laboratory experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.


Experiment 1
Experiment 2
Experiment 3
MEAN TIME SPENT OUT OF CREVICE (MIN)/ OBSERVATION PERIOD
70
60
50
40
30
20
10
0
SUCCESSFUL MALES
UNSUCCESSFUL MALES

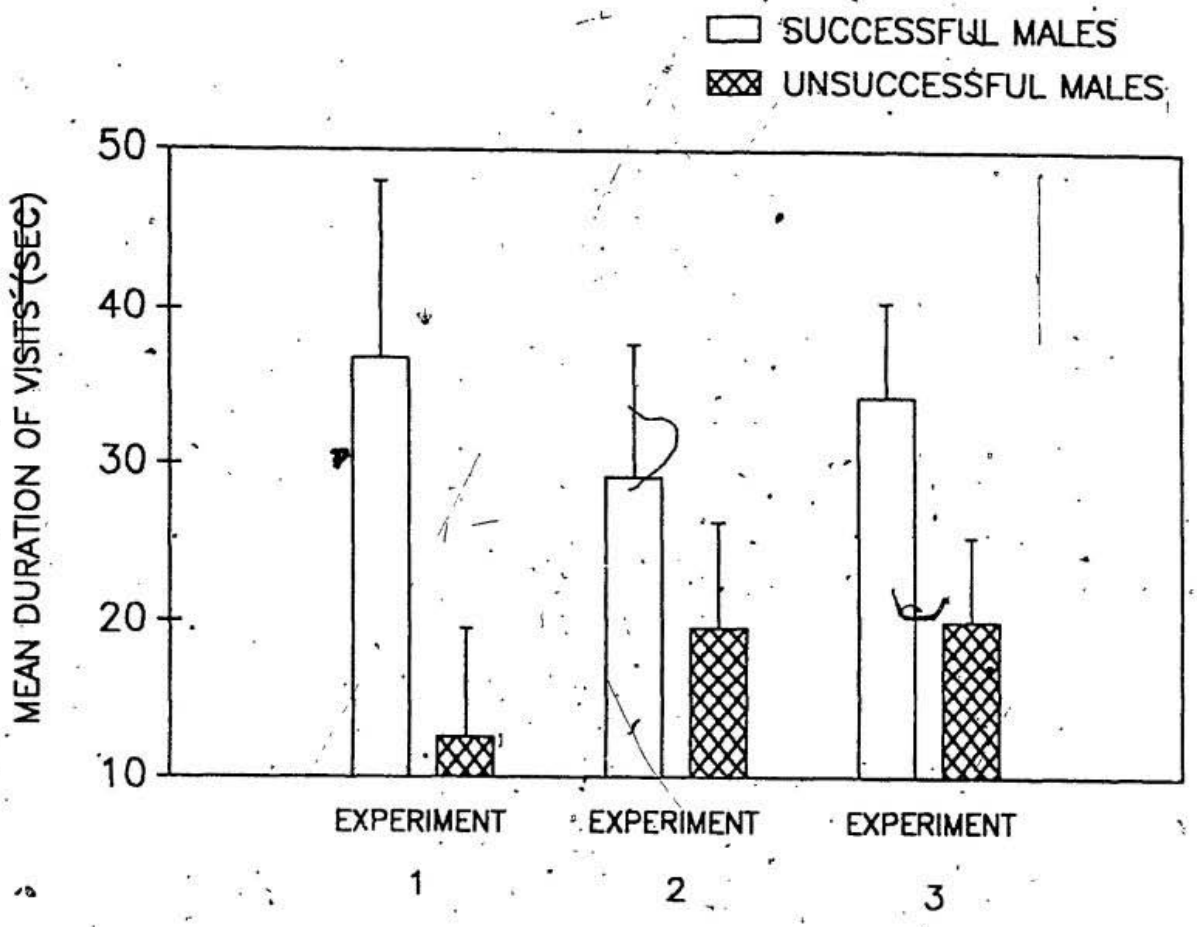
(q) 63 (b)

Figure 16: Comparison of the number of visits between success vs unsuccessful males in all three laboratory experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.


SUCCESSFUL MALES
UNSUCCESSFUL MALES
MEAN NUMBER OF VISITS/ OBSERVATION PERIOD
10
8
6
4
2
0
EXPERIMENT 1
EXPERIMENT 2
EXPERIMENT 3

64 (b)

Figure 17: Comparison of the duration of female visits between successful and unsuccessful males in all three experiments. Standard errors denoted by vertical bars. Successful and unsuccessful males defined in text.


SUCCESSFUL MALES
UNSUCCESSFUL MALES
MEAN DURATION OF VISITS (SEC)
50
40
30
20
10
EXPERIMENT 1
EXPERIMENT 2
EXPERIMENT 3

(q) 59

between introduction of the female and spawning. This is in contrast to Experiment 1 in which five of the six trials spawning took place before three days had elapsed. Overall, successful males had significantly more aggressive encounters (U= 50.0, $p<0.05$; Figure 11) which were longer (U= 46.3, $p<0.05$; Figure 12), and more intense (U= 24.5, $p<0.05$; Figure 13), than unsuccessful males. Successful males had a greater maximum distance response (U= 42.0, $p<0.05$; Figure 14), and spent significantly more time out of their crevices (U= 31.5, $p<0.05$; Figure 15) than unsuccessful males.

In all trials the most aggressive male, determined by the highest values for the measures of aggression, was successful in receiving all the spawnings in all the trials. The female visited all males at least once during the trial. However, in this experiment, differences between the spawning and non-spawning males in the number and duration of female visits were not as distinct. One successful male had significantly more visits than both other males (U=35.3, $p<0.05$; U= 29.5, $p<0.05$), but only longer in duration than one other male (U= 27.5 , $p<0.05$). One successful male had longer visits than both other males (U= 30.5, $p<0.05$; U= 25.6,$p<0.05$), but only more in number than one other male (U= 25.8, $p<0.05$). In run 3, the successful male had more visits than one other male (U= 30.7, $p<0.05$), and longer visits than the other male (U= 35.5, $p<0.05$).

Nevertheless, as a group, successful males received significantly more and longer visits than unsuccessful males ($U= 38.5$, $p<0.05$; $U= 35.9$, $p<0.05$; Figure 16 and 17, respectively).

Experiment 3.

In this experiment a total of three males and three females were tested. Due to the declining number of gravid females in the 1987 reproductive season, only one run with three trials was performed. In each trial, each male had one opportunity to be the "prior resident". Regardless of residency status, one male had significantly more aggressive encounters ($U= 21.0$, $p<0.05$; Figure 11) which were longer ($U= 29.1$, $p<0.05$; Figure 12), and more intense ($U= 24.1$, $p<0.05$; Figure 13) than both the other males. This male also had a greater maximum distance response ($U= 20.0$, $p<0.05$; Figure 14), and spent significantly more time out of his crevice ($U= 30.0$, $p<0.05$; Figure 15), than both other males. These relationships between males did not change regardless of which male was placed in the tank prior to the other two males.

The successful male had significantly more visits by the female ($U= 35.5$, $p<0.05$; Figure 16), which were longer ($U= 28.5$, $p<0.05$; Figure 17), than those of the two other males. However, each male was visited by the female at least once during a trial. One male received all three

spawnings in this trial.

2.3.2. Field Observations

The positions of all males, egg masses, and females along the transect in 1986 and 1987 are shown in Figures 7 and 8. The data from the 1986 and 1987 reproductive seasons were pooled for analyses unless otherwise stated. Appearance along the transect was not correlated with size regardless of sex (♀ & ♂, $r=0.13$, $N=42$, $p=0.12$; ♂ $r=0.28$, $N=23$, $p=0.33$; ♀ $r=0.11$, $N=20$, $p=0.10$). Hence, appearance at the spawning areas was not size dependent. However, it should be noted that the transect was only surveyed once per week during the spawning season and the return of all fish took place during a span of three weeks. The sampling schedule may not have been sensitive enough to evaluate these trends.

Through counts of the number of eggs from egg batches spawned in the laboratory the following relationship was developed between egg batch volume and the number of eggs in a batch:

$$\text{Egg number} = 88.401 + 65.21 * (\text{Volume of batch})$$

($r=0.87$, $N=17$, $p=0.03$). Subsequently, from measuring egg

batch dimensions in the field the number of eggs per batch could be estimated. In both 1986 and 1987 there was significant variation in male spawning success as determined by both the number of egg batches per male (1986, X^2= 20.01, N=13, $p<0.05$; 1987, X^2= 19.71, N=10, $p<0.05$; compared to poisson distribution), and by the number of eggs per male (1986, X^2= 41.36, N=13, $p<0.05$; 1987, X^2= 54.31, N= 10, $p<0.05$). Male size was not correlated with the number of egg batches (r=0.67, N= 23, p=0.11). However, male size was significantly positively correlated with the total number of eggs in the nest (r=0.84, N= 23, $p<0.01$). The largest males obtained the largest number of eggs. This suggests that large males are spawning with large females since female fecundity is dependent on female size (LeDrew and Green 1975). Temporal appearance on the transect was neither significantly correlated with male spawning success as determined by the number of egg batches (r=0.23, N=23, p=0.45), nor with the number of eggs per nest (r=0.41, N=23, p=0.12). Once again, the sampling of the appearance of fish on the transect may not have been sensitive enough to pick up the trend. Also, since a threshold spawning temperature of 4.0 C is needed (LeDrew and Green 1975; pers. obs.), those which return early cannot spawn.

Appearance of egg masses during the reproductive season was significantly correlated with male total length only in 1986 (r=0.69, N=13, p=0.05). This correlation might

indicate males which receive more eggs spawn earlier during the reproductive season. Since male size was also correlated with spawning success it might suggest large males are spawning earlier and receiving more eggs as compared to small males. This correlation was not evident in 1987. A more compressed spawning season may have altered the finding in 1987. Sea temperatures did not warm up to 4.0°C until late May 1987, and took only 10 days to warm to 6.0°C (Figure 18). Appropriate sea temperature for spawning may not have occurred gradually enough for the sequence of spawning to occur.

Male total length was found to be positively correlated with the mean number of response to the model intruder ($r= 0.78$, $N=10$, $p<0.05$; Figure 19) and the mean distance of responses to the model intruder ($r= 0.88$, $N=10$, $p<0.05$; Figure 20) during the pre- and reproductive periods (April--July). The post-reproductive period was not included in this regression since during this time there was essentially no response to the model intruder by either sex, regardless of size (See Chapter 1). Furthermore, for at least half of the post-reproductive period fish were not present on the transect (See Chapter 1).

In summary, field results indicate large males are more aggressive and receive more eggs in total, than small males.

Figure 18: Water temperatures during the 1986 and 1987 spawning seasons at Bellevue, Trinity Bay.

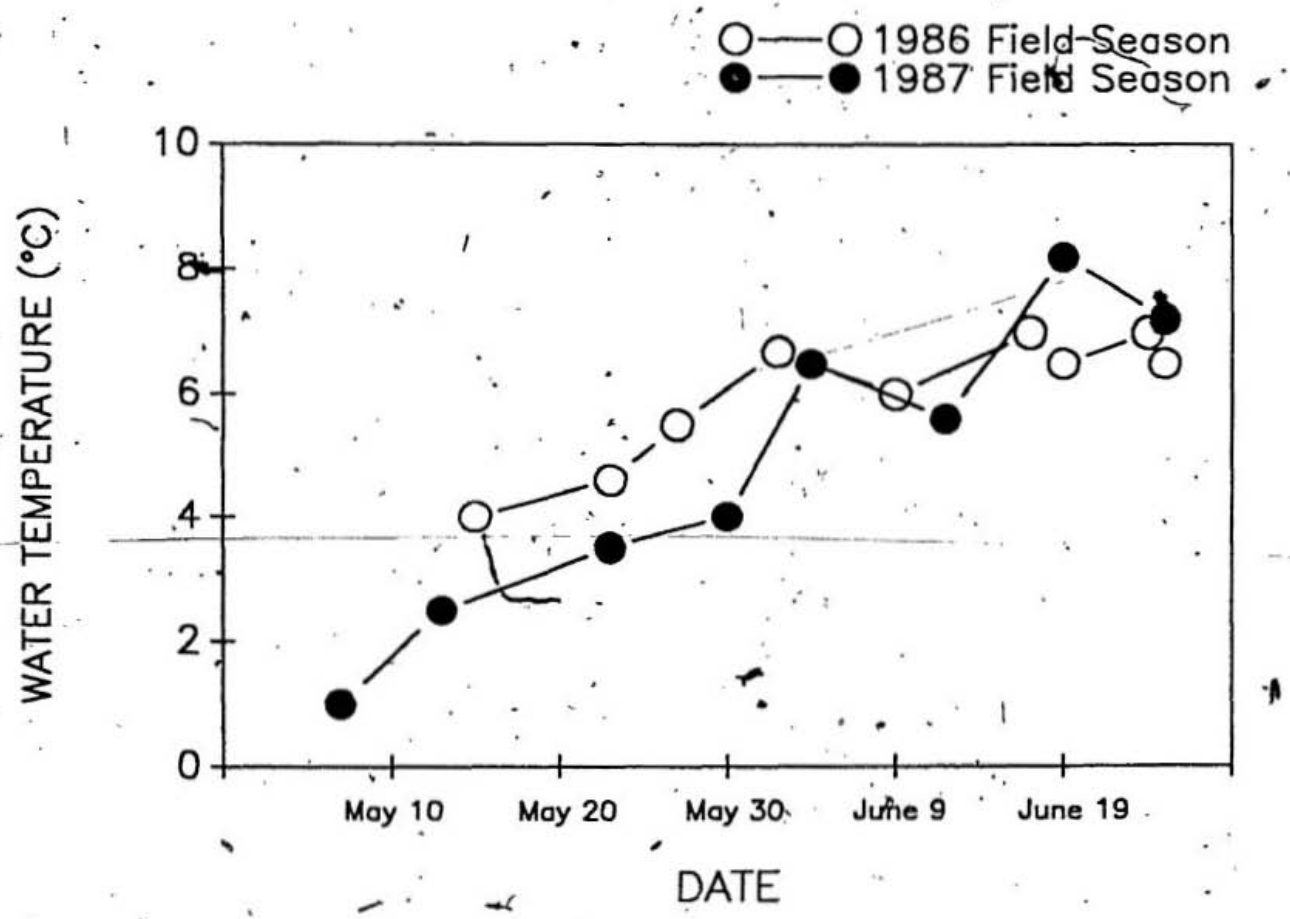

1986 Field Season
1987 Field Season
WATER TEMPERATURE (°C)
10
8
6
4
2
0
May 10
May 20
May 30
June 9
June 19
DATE

Figure 19: Mean number of responses to the model intruder vs total length (cm) of male fish on field study site during the 1986 and 1986 field seasons.

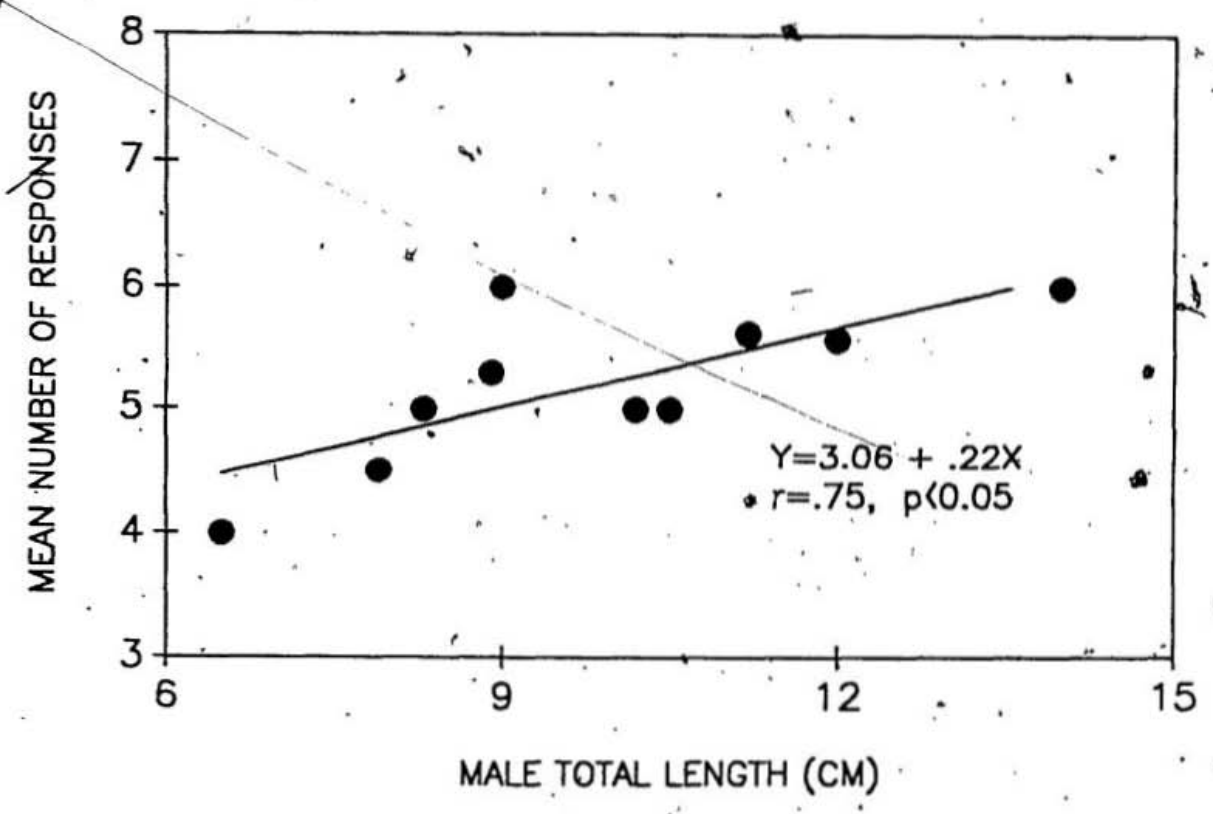
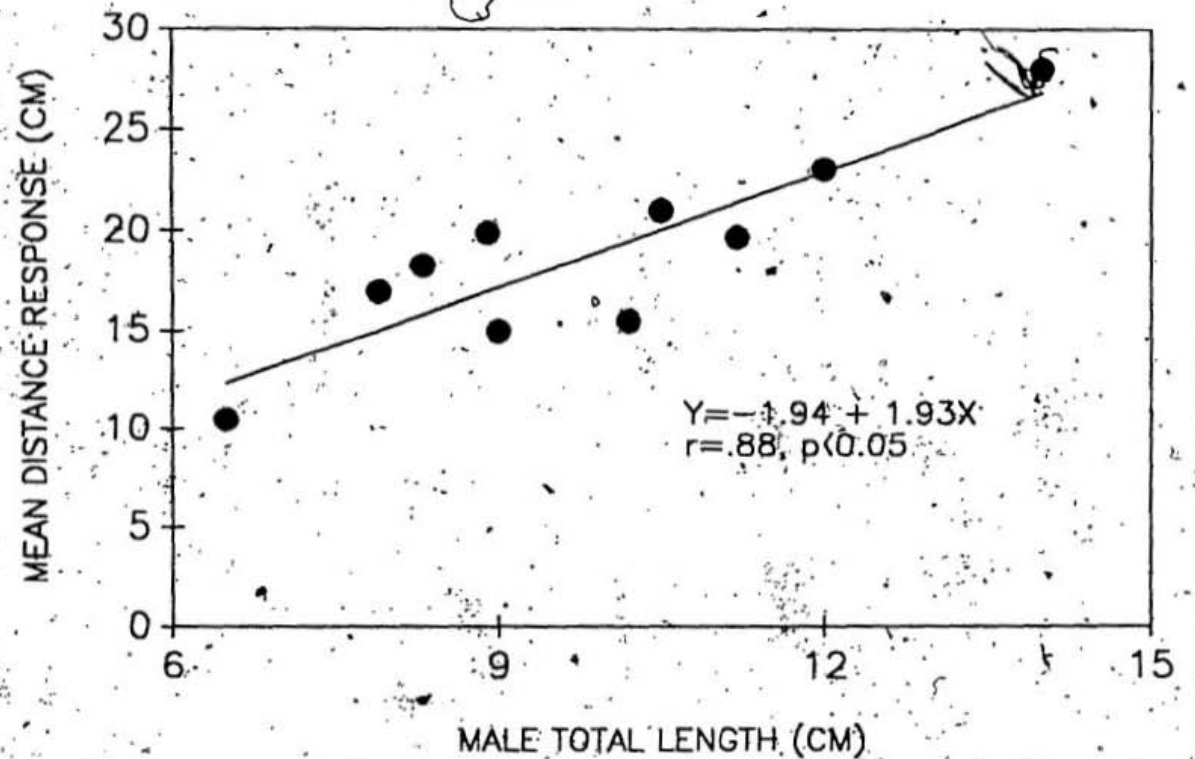

MEAN NUMBER OF RESPONSES
8
7
6
5
4
3
6
9
12
15
MALE TOTAL LENGTH (CM)
Y=3.06 + .22X
r=.75, p<0.05

Figure 20: Mean distance (cm) response to the model intruder vs total length (cm) of male fish on field study site during the 1986 and 1987 field seasons.


MEAN DISTANCE RESPONSE (CM)
30
25
20
15
10
5
0
6
9
12
15
MALE TOTAL LENGTH (CM)
Y=−1.94 + 1.93X
r=.88, p<0.05

73(b)

2.4. DISCUSSION

When males provide resources, females, when selecting a mate, should be influenced by the quality of the resource and by the quality of the defending male (Emlen and Oring 1977). This choice will lead to variance in mating success in the sex being chosen (Trivers 1972).

Among marine, territorial egg-guarders mating success has been studied in the damselfish, triplefin, and the lumpfish. In all species there was considerable variation in mating success (Schmale 1981; Thresher and Moyer 1983; Goulet et al. 1986; Thompson 1986). The present laboratory and field study indicates significant variation in male mating success in the radiated shanny, U. subbifurcata. Since females travel to male territories to spawn, much of this variation may be generated by female preference. The question of which male characteristics contribute to mating success becomes of interest.

In the present study, in both laboratory and field experiments, large males obtain more eggs per reproductive period than small males. Moreover, large males are more aggressive than small males. Note that age and growth were not separated as components of size in this study. Male mating success has previously been shown to be correlated with male size in the mottled sculpin (Downhower and Brown 1980; Brown 1981), the cichlid, Cichlasoma nigrofasciatum,

(Noonan 1983; Keenleyside et al. 1985), the damselfish, Glyphidodentops cynaeus, and Eupomacentrus patritus (Schmale 1981; Thresher and Moyer 1983), and the triplefin, Forsterygion varium, (Thompson 1986). Male mating success has been shown to be correlated with male aggressiveness in the johnny darter, Etheostoma nigrum (Grant and Colgan 1983).

Both laboratory and field results suggest that prior residency is unimportant in female mate choice in the radiated shanny. Thus, returning to inshore nesting areas first does not imply increased spawning success in the reproductive period. This is not surprising because returning to nesting areas first, when water temperatures are not yet warm enough to spawn, may only allow choice of crevice sites. In the field, crevice/nest quality did not appear important in female mate preference. Also, for males, it does not appear there is a sequence to returning to the study site based on size or aggressiveness. However, there may be a hierarchial order to spawning based on male size. Large males spawned earlier than small males in 1986. The more compressed 1987 reproductive season may have eliminated this sequence by reducing the available spawning time for all shannies.

Why do females choose large, aggressive males? Howard (1978a) described two types of male quality: 1) characteristics, such as parental care, that provide

immediate gains to the female in terms of her offsprings' survival; and 2) phenotypic markers of genetic quality that may affect the fitness of her offspring (i.e. body size as an indicator of survival or competitive ability- McCauley and Wade 1978). Additive genetic variance for male quality may be rapidly selected out of a population in a polygynous species; so females may not be able to assess type 2 male attributes (Maynard Smith 1978; Thornhill 1979). Genetic quality of the male may therefore, be less important in influencing male choice than factors which directly affect the survival of the females' offspring. Therefore, female U. subbifurcata may prefer large and aggressive males if the latter are more effective egg guardians. The fact that larger males make better egg guardians underlies female mate preference in mottled sculpins (Brown 1981), and some cichlids (Keenleyside et al. 1985). Grant and Colgan (1983) in a study on the johnny darter discovered that by choosing a more aggressive male (one with a high maximum distance response) females increased their fitness because males with a high maximum distance response to females were better able to defend their eggs. Consequently, female U. subbifurcata may choose large aggressive males to enhance survival of her reproductive investment and subsequent inclusive fitness.

Although females in this system choose the largest, most aggressive male, it appears size is a less ambiguous cue than is aggressiveness. Both male size and aggression

can be assessed by the female using size alone since male size was found to be positively correlated with male aggression. Also, in the laboratory experiments, it took females longer to spawn when introduced to three males of similar size than when introduced to three different sized males. Nevertheless, females are able to assess male aggression alone. Although it did take more time, females choose the most aggressive male when presented with three males of similar size in the laboratory experiments. Hence, both male size and aggression must be evaluated by the female.

How do females assess male quality? Unlike the majority of intertidal fishes described to date, no obvious courtship has been recorded for U. subbifurcata (Green et al. 1988; pers. obs.). It is highly unlikely that visual cues are important since the nocturnal habits of the shanny would reduce the efficiency of visual displays. In addition, the radiated shanny does not spawn in a manner which would allow for female observations of male/male competition. All male competition occurs prior to spawning regardless of female presence. Also, females cannot assess male aggressiveness by instigating an encounter with a potential spawning partner since males do not show aggression to females during the reproductive period. Consequently, the female cannot assess male aggressiveness visually. Apart from visual cues, females may be able to

assess male aggressiveness by pheromones. Correlational studies combined with traditional removal and replacement experiments have confirmed the involvement of the endocrine system in the regulation of reproductive behaviour in fish (Liley et al. 1987). Further, sex pheromones have been known to be released as a result of the reproductive or behavioural state of a fish (Stacey et al. 1987). Recent studies have demonstrated that the use of pheromones of blennoid fishes is common (Gibson 1982). If increases in the level of aggression in male shannies were associated with increases in levels of pheromones, females could assess male aggressiveness. Female choice would then be "error-proof" since there are no mechanisms whereby males can alter their physiology and endocrine system to fool females. Large males which were not aggressive could not deceive females into spawning. Hence, this strategy would be an evolutionary stable strategy (ESS; Maynard Smith 1978). Further work is necessary to evaluate the importance of pheromones in mate choice in this species.

Although female choice exists in the radiated shanny, theory would also predict some male mate choice since male investment goes beyond gamete production to nest guarding and parental care of the offspring (Trivers 1972). By the fact that females are monogamous, and are reproductively spent after one spawning, a mating mistake can affect the season's entire reproductive success. Alternatively,

because males are polygynous, one "bad mating" will not affect the season's reproductive success. Consequently, it might be expected that males attempt to increase their mating success by maximizing the number of spawnings. However, because male total length was found to be positively correlated with the number of eggs in the nest, and not the number of batches, suggests that large males are spawning with large females. However, large males are not obtaining more batches than small males. It would appear large males are obtaining high numbers of eggs by mating with large females since female fecundity is dependent on female total length (LeDrew and Green 1975).

The simplest explanation for why male shannies may prefer larger females is that they attempt to maximize the number of eggs they obtain per unit time during the reproductive period. This will be particularly important if there is a foraging cost associated with egg guarding resulting in significant weight loss (Coleman et al. 1985). Male shannies should attempt to maximize their rate of obtaining eggs. However, there are alternative explanations for male preference for large females. If female shannies cannibalize eggs already in the nest and their impact on egg predation is not size dependent, males may prefer larger females, because they yield more eggs per unit risk to eggs already present. Loiselle (1982) suggests that this explains male preference for larger females in the pupfish,

Cyprinodon macularius calforniensis. Another explanation is, if there is a significant cost to male ejaculation (e.g. Nakatsuru and Kramer 1982), males should prefer larger females, since the latter will provide more eggs per ejaculate. However, since females also prefer to spawn with large males , one should expect spawning partners in the wild to be of similar size (i.e. positive assortative mating).

The mechanisms of choice are poorly documented in the literature. Traditional mate choice studies have discovered male traits which influence female choice through correlational studies of male mating success and male characteristics. The female and mechanisms of female choice have either been unidentified or ignored. The present study showed that although male/male competition occurs, females actively examined males and nest sites through visits and chose the largest and most aggressive males in laboratory experiments. The order of visits were documented, but the sample sizes per observation period were too small to determine any statistical pattern to the visits. Brown (1981) devised a computer simulation model to examine the mechanisms of choice. Results of the computer simulation of female choice in which females mated with a male who was larger than or equal to the last male encountered are consistent with many of the observed patterns of male spawning success. Brown (1981) assumed females only

remember the qualities of the last male encountered when evaluating a potential spawning partner. Observations on the radiated shanny did not show such a simple pattern. Females visited males more than once and could have evaluated the quality of three males. Further, a pattern of one male being used as a reference would have been observed as one male being visited every second visit. This pattern was not seen in the radiated shanny. It would be interesting to extend the mate choice experiments in this study by continually adding one male to an experiment and determining at what number of males, females are no longer able to visit all experimental males.

In summary, female U. subbifurcata choose large, aggressive males which presumably make better egg guardians and subsequently increase survival of offspring. Females actively visit males and their nests before spawning. Pheromonal cues for female choice, although speculative, seem highly likely in this nocturnal fish. Finally, males also choose large females which results in observed positive assortative mating.

SUMMARY

In the laboratory, Ulvaria subbifurcata maintained exclusive use of a crevice site for 12 months, with no crevice sharing or switching. Hence, the crevice site can be considered a territory. From late March to early November, at the study site in Bellevue, Trinity Bay, adult shannies had exclusive use of a crevice site which was actively defended. However, in winter, adult shannies left their crevice sites and moved offshore.

The function of territoriality in the radiated shanny can be ascribed to shelter and reproduction. Shelter is particulary important for small intertidal fishes which are incapable of sustained swimming. Territoriality for reproduction in female radiated shannies appears secondary to shelter. During the reproductive period females search for males and deposit eggs in the males' territory. Consequently, shelter from predators during the spawning period is essential. Territoriality in male radiated shannies is essential for reproduction as it allows males a location to spawn and guard eggs.

Aggression in both sexes of the radiated shanny appears to be important for territoriality and reproduction. Aggression began to increase during the pre-reproductive period (March - April) and peaked ruing the reproductive period (May - July) for both sexes. A proportion of the

increase in aggression in the pre-reproductive period can be attributed to territory establishment in the field. However, the fact that the increase is also recorded in the laboratory suggests that increased GSI and hormonal levels during the reproductive period could be a proximate cause for the increase in aggression. Hence, aggression is important in the reproductive behaviour of the radiated shanny.

More specifically, aggression appears to play an important role in mate choice in Ulvaria subbifurcata. In both laboratory and field observation there was variation in male spawning success. The largest and most aggressive males received the most eggs per reproductive season. As well, the largest and most aggressive males may be receiving their eggs earlier in the season than small less aggressive males. Although, males compete amongst themselves through aggressive encounters (intrasexual selection) females actively examined males and nest sites through nest visitations and chose the largest and most aggressive males (intersexual selection).

In summary, aggression in U. subbifurcata appears to play an important role in territoriality and sexual selection, two important aspects of sociability.

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Appendix 1: Glossary of the agonistic MAPs displayed by adult Ulvaria subbifurcata (Green et al. 1988).

Approach: A MAP in which one fish orients to and either swims slowly towards or "walks" (using pectoral fins) towards another fish.

Lunge: A rapid forward movement of one fish towards another. The caudal and pectoral fins are used in this MAP.

Bite: A contacting MAP where one fish closes its jaw on another fish.

Back-up: A backward movement where the fish uses the pectoral fins and reverse propagation of an anquilliform wave.

Flee: Rapid swimming of one fish away from another fish.

Chase: Rapid swimming of one fish after a fleeing fish.

Frontal Display:

Gape: A display MAP in which the displaying fish is oriented towards another fish with the mouth open. Occasionally the opercula would be extended.

Opercular Flare: A display MAP associated with Gape. While oriented towards another fish, the displaying fish would extend the opercula. This MAP, as well as Gape, was observed to be performed at various intensities as indicated by the degree of opercular extension and mouth Gape. In the most intense Gape and Opercular Flare, the mouth would be open to its maximum and the opercula extended so that the brachiostigals could be seen.

Dorsal Fin Erection: A display MAP in which the dorsal fin rays are at an angle of approximately 90 to the longitudinal axis of the body, causing the dorsal fin spot to assume a circular shape.

APPENDIX 1 (con't)

Dorsal Fin Flap:	A display MAP in which the dorsal fin lies flat on either the right or left side of the fish.
Dorsal Fin Wave:	A display MAP in which the position of the dorsal fin is similar to that in the Dorsal Fin Flap except that the fin is moved from the leading edge posteriorly using wave propagation.
Pectoral Fin Fan:	A display MAP which involves a rapid lateral dorsal to ventral quivering motion of the pectoral fin.
Shake:	A display MAP in which the posterior end of the displaying fish's body is curved sharply to either the left or right and straightened quickly. This causes a jerking motion which may or may not result in forward movement.
Turn Away:	A MAP which occurs when two fish are orienting towards one another and one fish moves its head to the right or left.

Appendix 2: Growth, change in total length (TL, cm), of all fish throughout year and yearly means of all aggressive measures for each fish used in a multiple regression and correlation matrix of variables in regression.

FISH	SEX	TL START	TL END	TL DIFF	x AGG	x INT	x DUR	x TSN
1	F	8.3	8.4	0.1	0.09 (0.01)	1.00 (0.00)	4.67 (0.03)	3.54 (0.38)
2	F	8.6	8.6	0.0	0.10 (0.02)	1.50 (0.35)	7.96 (3.14)	4.41 (0.43)
3	M	8.1	8.2	0.1	0.20 (0.05)	2.50 (----)	14.27 (----)	4.84 (0.47)
4	M	8.4	8.7	0.3	0.40 (0.20)	1.90 (0.21)	7.68 (1.57)	7.11 (0.56)
5	F	10.1	10.1	0.0	0.15 (0.02)	1.50 (0.35)	13.26 (6.96)	10.30 (0.64)
6	F	9.6	9.9	0.3	0.20 (0.04)	1.00 (1.00)	4.58 (4.58)	0.71 (7.11)
7	M	10.1	10.2	0.1	0.25 (0.03)	1.63 (0.24)	7.05 (1.28)	8.37 (0.49)
8	M	10.2	10.4	0.2	0.75 (0.06)	1.52 (0.05)	18.38 (2.02)	13.20 (0.64)
9	F	9.0	9.6	0.6	0.03 (0.03)	1.00 (0.00)	10.80 (1.06)	5.81 (0.13)
10	M	8.7	9.5	0.8	0.14 (0.01)	1.11 (0.04)	23.06 (0.69)	5.69 (0.12)
11	M	8.7	9.4	0.7	0.31 (0.01)	1.43 (0.04)	21.24 (0.70)	7.98 (0.14)
12	F	11.6	13.0	1.4	0.83 (0.00)	1.00 (0.00)	24.57 (3.01)	7.02 (0.13)
13	F	11.4	12.0	1.4	0.18 (0.01)	1.00 (0.06)	22.03 (1.02)	8.43 (0.14)
14	M	11.0	12.8	1.8	0.41 (0.06)	1.73 (0.03)	29.03 (0.63)	10.03 (0.15)

APPENDIX 2 (Con't):

CORRELATION MATRIX:

	GROWTH	SEX	TOTAG	INT	DUR	TSN
GROWTH	1.00	0.15	0.19	0.02	0.81	0.31
SEX	0.15	1.00	0.67	0.60	0.37	0.37
TOTAG	0.19	0.67	1.00	0.43	0.35	0.79
INT	0.02	0.60	0.43	1.00	0.14	0.21
DUR	0.81	0.37	0.35	0.14	1.00	0.49
TSN	0.31	0.37	0.79	0.21	0.49	1.00

AGG= number of aggressive encounters; INT= intensity of aggressive encounters; DUR= duration (sec) of aggressive encounters; TSN= time (min) spent out of nest.

Multiple linear regression equation:

GROWTH = 0.0578 * DUR - 0.2677

No other variables entered as significant factors ($p > 0.10$)

Appendix 3: Length and sex of fish on Bellevue transect during 1986 and 1987.

YEAR	1986		1987		
FISH	TOTAL LENGTH (CM)	SEX	FISH	TOTAL LENGTH (CM)	SEX
1.	7.0	♂	1.	12.0	♂
2.	6.5	♂	2.	10.2	♂
3.	8.0	♀	3.	7.9	♀
4.	14.0	♂	4.	8.9	♀
5.	7.5	♂	5.	10.9	♂
6.	10.5	♀	6.	8.3	♂
7.	8.0	♂	7.	8.9	♂
8.	8.5	♀	8.	10.1	♀
9.	10.5	♂	9.	7.8	♀
10.	9.0	♂	10.	7.9	♂
11.	10.0	♂	11.	15.1	♂
12.	13.5	♂	12.	10.9	♂
13.	10.5	♂	13.	7.7	♀
14.	7.9	♀	14.	8.9	♀
15.	8.4	♀	15.	9.1	♀
16.	9.6	♀	16.	10.1	♀
17.	10.9	♀	17.	9.9	♀
18.	11.0	♀	18.	10.9	♂
19.	7.8	♀	19.	12.1	♀
20.	8.8	♀			
21.	9.8	♂			
22.	7.9	♂			
23.	11.0	♀			

Appendix 4: Results of activity-level counts showing number of fish seen outside of crevice during dusk/high tide, dusk/low tide, afternoon/high tide, and afternoon/low tide, at the Bellevue study site.

	DUSK	AFTERNOON
HIGH TIDE	36	27
LOW TIDE	15	8

Appendix 5: Summary of all males and females used in all experiments of male choice.

SEASON	EXP.	RUN	MALE (cm)	FEMALE (cm)	SPAWNING PARTNER
1986	1	1	1. 13.0 2. 11.9 3. 9.8	10.6	1.
				10.6	1.
				9.4	1.
	1	2	4. 12.6 5. 11.8 6. 9.8	9.9	4.
				10.9	4.
1987	2	1	7. 8.2 8. 8.3 9. 8.1	7.6	8.
				7.3	8.
				8.1	8
	2	2	10. 8.7 11. 8.6 12. 8.9	8.7	11.
				7.2	11.
				8.5	11.
	2	3	13. 15.2 14. 15.0 15. 14.9	7.9	13.
				8.2	13.

Appendix 5 (con't)

3	3	16. 8.7 17. 8.5 18. 8.6	8.7	18.
			8.6	18.
			7.2	18.